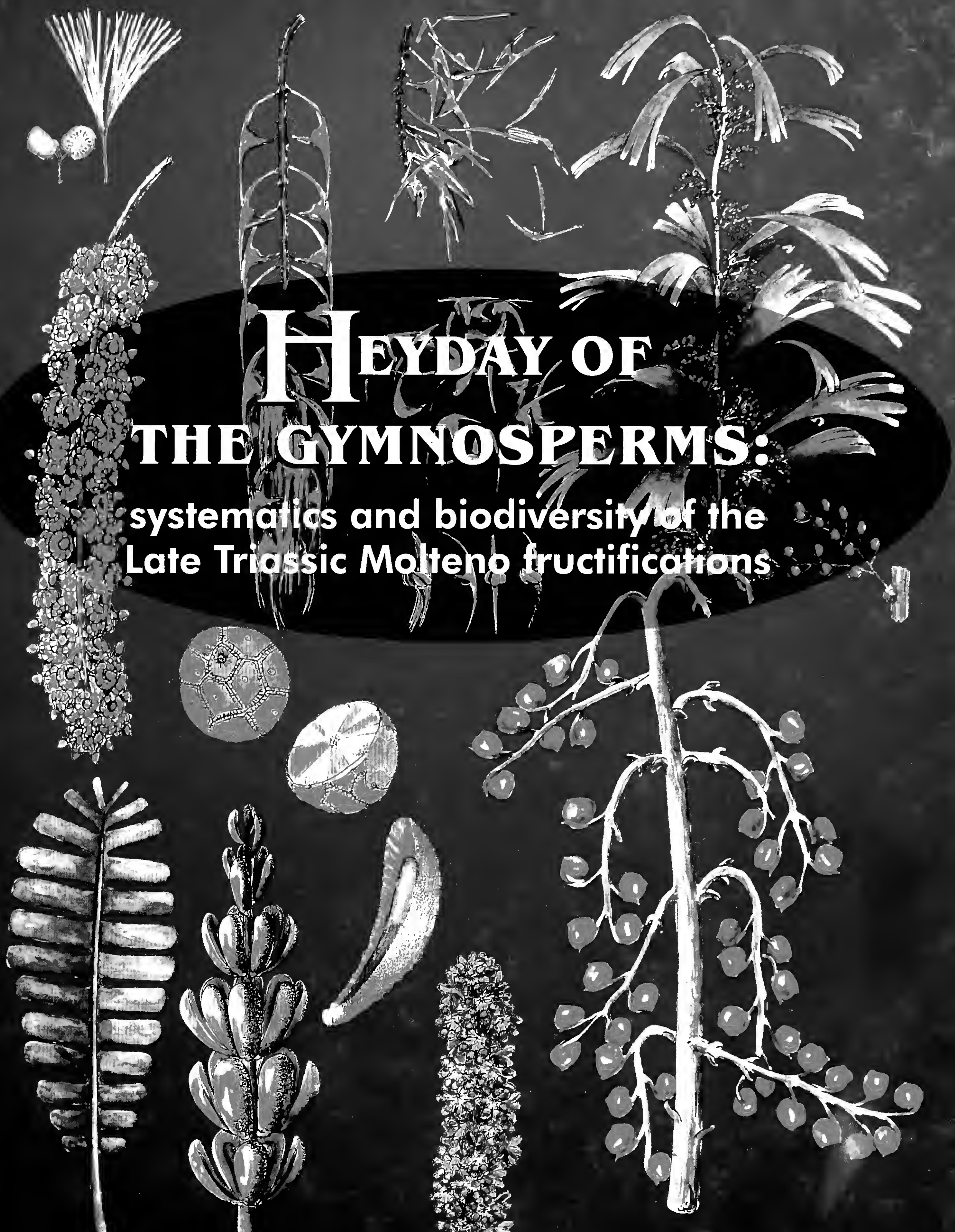
HEYDAY OF THE GYMNOSPERMS:

systematics and biodiversity of the Late Triassic Molteno fructifications



John M Anderson & Heidi M Anderson

STRELITZIA 15

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Heyday of the gymnosperms: systematics and biodiversity of the Late Triassic Molteno fructifications

by

John M. Anderson and Heidi M. Anderson

NATIONAL BOTANICAL INSTITUTE

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STRELITZIA

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* See *Bothalia* 28: 271–297 (1998).

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FOREWORD

Despite the bewildering diversity of living plants, it is remarkable that the overwhelming majority are representative of a single supremely successful clade: the flowering plants (angiosperms). These species range from grasses to baobabs, but as descendants of a single common ancestor they share fundamental similarities, and in a sense are merely different manifestations of the same relatively recent evolutionary diversification. Where flowering plants came from is a long-standing enigma in plant evolutionary biology, but over the last two decades a key advance has been the realisation that resolving the origin of flowering plants—at least conceptually—is a straightforward issue. What we need to know is: how are flowering plants phylogenetically related to other groups of seed plants?

The greatest single obstacle to answering this question is our ignorance of the diversity of other groups of seed plants (gymnosperms). Today, we have available to us only four non-angiosperm groups—cycads, conifers, Gnetales and *Ginkgo*—all of which are relatively well understood. In the past, however, the palaeobotanical record shows clearly that there were once many other gymnosperm groups that are now extinct. The inescapable conclusion is that the four groups of living seed plant are a very poor and unrepresentative sample of all the different kinds of seed plants that have ever existed.

This remarkable book on the gymnosperms of the Late Triassic Molteno flora by John and Heidi Anderson is a major contribution to understanding the diversity of seed plants that existed in the past. It joins the earlier works by the same authors in reflecting two lifetimes dedicated to exploring the biodiversity of the past so as to better illuminate the biodiversity of the present.

Based on extensive fieldwork in the Karoo Basin of South Africa, and huge collections (more than 27 000 catalogued slabs) from almost 70 localities, this book provides the most comprehensive insight so far into extinct seed plants from the Mesozoic of the Southern Hemisphere. Especially valuable is the use of large numbers of specimens to delimit species, the careful note taken of associations between different fossil species, and the quantitative approach to sampling. I am not aware of any other set of fossil assemblages that has been collected with such intensity, such uniformity of approach and such care.

A key feature of this book is the focus on fossil seed plant reproductive structures, which are represented by 35 genera and more than 80 species. This component alone represents a huge expansion to our knowledge of Mesozoic gymnosperms and provides the essential foundation for more detailed studies focused on individual taxa in the future. Especially important are those instances in which it has been possible to link ovulate structures, pollen-producing organs and leaves. As detailed follow-up work is done, these plants will become among the best-known plants in the Mesozoic and they will have a significant impact on future ideas of seed plant phylogeny and evolution.

Beyond its importance for systematic and phylogenetic studies, this book paints a vivid picture of the exuberant diversity of life in the Molteno flood plain, 230 million years ago. It reflects a world quite different, and in many respects more modern, than that of the Palaeozoic. It shows the re-emergence of biotic diversity in the shadow of the Permian extinction, and documents the habitats in which modern groups such as mammals, conifers, and beetles were beginning to come to the fore. But it is still a world without flowering plants and many other modern groups. As such it places our Recent condition in context and provides important clues as to how the modern world came about.

By any measure, John and Heidi Anderson's dedication to unlocking the secrets of the Molteno Formation has been extraordinary and the result has been a landmark contribution to palaeontology. This book and its previously published companion volumes will be of lasting value to anyone interested in the biology and ecology of the Mesozoic. More generally, it provides an indispensable glimpse into a pre-flowering plant world for anyone curious about plants of the past.

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24 October 2002

PREFACE

It was 35 years ago, in March 1967, that I ventured for the first time into Molteno territory. From then till now the world has changed. It has shifted—dramatically—in virtually every respect: man has stood on the moon and looked back at this only known living planet; we have come out the far end of the Cold War and of the Apartheid era; and we have entered a new communications era, the e-era, as overwhelming as that unleashed by Guttenberg's printing press in 1454. Most importantly of all, from our perspective, the human population has doubled from 3 billion to 6 billion persons in this time, and we have belatedly become aware of the *Sixth Extinction* of life globally. In 1967 continental drift was only a fringe hypothesis and concepts such as biodiversity and biophilia were still well in the future. It is, indeed, only in the last decade since the time of the First Earth Summit (Rio 1992) that the conservation fraternity has markedly expanded and begun expressing severe concern at the decimation of life everywhere, across the continents and throughout the oceans. The world has indeed changed. The falling of the Berlin Wall and the holding of the Rio Summit virtually coincided. The political, economic and social energy, so totally chained to the dread of nuclear annihilation can now be focussed on a new, no lesser dread, the extinction of diversity loosed on our planet by ourselves.

Back in the late 1960s when we began the long haul of amassing close on 30 000 catalogued slabs from 100 Molteno taphocoenoses, we had no thought of biodiversity—nor did anyone else. As the years rolled by and the number of localities discovered and sampled grew, and as the number of fossiliferous slabs accumulated, I became simultaneously aware of the prodigious extant biodiversity in South Africa. Through a parallel project on indigenous tree distributions I became woefully aware of the increasing pace of destruction through human disregard of our biosphere. In searching back and forth through geological and historical time, my awareness of the vicissitudes in the wealth of nature grew synergistically. Living in the present time frame and working through past time frames lends a sense of reality beyond oneself.

The Molteno became, increasingly, a lot more than merely an exercise in collecting and describing fossils. It became for me far more than a tally of papers published per year, far more than the taxonomy of plants dead and buried 200 million-years ago. It became part of a multifronted obsession to help swell our awareness of biodiversity trends through time, and to impact somehow on mankind's collision with that diversity as it exists today.

This has meant spreading widely, perhaps too thinly. It has meant, for one, that this volume on the Molteno gymnosperms—*Heyday of the gymnosperms*—has taken a decade or two longer to appear than it might have done. It has meant, also, a few stout monographs instead of numerous slender papers in journals. So be it: in our lives as lived in linear time, we can hope to have some affect on the future, but not the past.

We have learned about ceaseless change and about ubiquitous interdependence; about the many starts and the fewer enduring branches in the tree of life—all of life—including our own individual lives. We *are* one with nature. Here then, in this volume and its sequels, is the Molteno gymnosperm story as currently known. Here is how it meshes with and contributes to the broader picture of the evolution of life.

John M. Anderson
14 January 2002

ABSTRACT

A comprehensive study of the gymnospermous element of the Late Triassic Molteno Fm., Karoo Basin, South Africa—based on a collection of 27 000 catalogued slabs from 100 assemblages (taphocoenoses)—is concluded with the current volume whose focus has been very largely on the reproductive structures. This has revealed a diverse flora including 20 genera (51 species) of ovulate fruit, 15 genera (35 species) of microsporangiate fruit and 27 genera (113 species) of foliage, representing an estimated combined whole-plant total of 38 genera (143 species) in 32 families, 23 orders and 10 classes of gymnosperm. A high proportion of the female and male fruit genera (and species) are described as new, while as many as 10 orders and 11 families are newly instituted. Of particular interest are new families such as the Fredlindiaceae (based on the whole-plant *Fredlindia/Halley-octenis/Cycadolepis*) and Lindthecaceae (*Lindtheca/Taeniopteris*), shedding new insight on the earliest evolutionary radiation of the class Bennettitopsida; and the Antarctic order Petriellales (with *Kannaskoppia/Kanna-skoppifolia/Kannaskoppianthus* from the Molteno) whose nearest affinities appear to lie with the Eurasian Caytoniales. In spite of the relatively intensive and extensive sampling of the formation and the rigorous approach towards identifying female/foliage/male affiliations, around half of all organ-genera remain without any suggestion of affiliates and few are decisively established. Concluded from this is that the taphonomic filter is severe, and that a significant proportion of the plant-genera colonising the Molteno Biome remain uncollected or were never preserved.

In order to place, systematically, the rich spectrum of new reproductive gymnosperm taxa found in the Molteno, it has been necessary to prepare a revised global classification of the gymnosperms. This will be published as sequels to the current volume. The classification is based, conceptually, on the ovulate fruit alone—with a total of 8 classes, 37 orders and 76 families from the Late Devonian to present being recognised. The significance with regard to Molteno systematics is the pattern of diversity trends that is revealed. At family and order level there is seen a clear diversity low in the earliest Triassic and an equally clear peak (the 34 families being twice the number recorded for any other interval) in the Late Triassic. It is from this evidence that we propose the later Triassic as representing the heyday of the gymnosperms.

The Molteno Fm., as currently understood, provides the clearest available window globally onto the explosive radiation of plant (and insect) life through the Triassic: it was the rapidly evolving ecosystems of this interval following the end-Permian extinction that spawned the earliest mammals, dinosaurs and very possibly the stem-angiosperms.

GUIDE TO THE LAYOUT OF THIS VOLUME & SEQUELS

The primary aims of this study (including its sequels) are to describe the remarkable spread of gymnospermous fruit, many of which are new and unique, discovered in the Molteno Formation; to place these in context within a comprehensively revised classification of the gymnosperms globally; and to draw attention to the peak of biodiversity characterising the Late Triassic. The work is planned to comprise two or three parts, with several sections, as follows.

THIS VOLUME

Molteno sampling, floristics & biodiversity

The purpose here is to provide a succinct backdrop to the systematics section. We present, largely in the form of tables, vital statistics on the 100 sampled taphocoenoses on the one hand and results in terms of floristics, classification and diversity on the other. The main thrust on Molteno biodiversity—with the far-reaching insights this lends globally—is everywhere reflected.

Systematics of the Molteno gymnosperms

This section forms the core, and bulk, of the volume. Though the emphasis is on the systematic description of the ovulate and microsporangiate organs from the Molteno, the gymnospermous foliage is also covered. A comprehensive account of the Molteno gymnosperms, in classified sequence, is presented (see classified list on pp. 54, 55). Introductory sections outline format and taxonomic approach, and include a pictorial glossary of morphological terminology. To lay stress on natural diversity, the affiliation of fruit and foliage within the framework of the Molteno Biome, and its seven recognised habitats, remains a guiding principle throughout. Concise, comparative text accompanied by the liberal use of pen sketches and photographic plates follows the style of our previous monographs on the Molteno and other South African palaeofloras (And. & And. 1983, 1985, 1989).

A total of 35 organ-genera (22 new) and 86 organ-species (79 new) of gymnospermous fruit, within an overall 32 whole-plant families (11 newly named) and 23 whole-plant orders (10 newly named), are described from the Molteno. (It must be emphasised that families and orders are formally instituted and named here only on the basis of ovulate—not microsporangiate or foliage—genera.)

SEQUELS TO CURRENT VOLUME

A Molteno overture

In this full-colour section, the purpose is to present an impressionistic picture of the Molteno Biome: its climate, habitats (ecozones), flora, insect fauna, and, most particularly, the nature of the gymnospermous element of the flora. The focus on the latter is threefold: the diversity witnessed firstly amongst the female cones, secondly amongst the male cones, and thirdly at whole-plant level in distinguishing families and orders.

Whole plants: an exploration of habit & habitat

We have to date recognised 16 multi-organ genera in the gymnospermous fraction of the Molteno flora. Included are those cases where affiliations between foliage and female and/or male fruits have been established with some measure of reliability. Emphasis is on Molteno distribution patterns, seasonality of production, and the reference taphocoenoses—largely towards assessing the habit and favoured habitat of the species differentiated within each genus.

Global classification of the gymnosperms

In view of the unsettled status of gymnosperm classification, fossil and extant, we have felt compelled to attempt a global revision of the division to provide a meaningful context for the many Molteno taxa. To enhance the integration between the Molteno and global gymnosperms and for general usability, we have elected to fully illustrate the classification. This compilation, including first and last occurrences of all families, builds largely on Cleal (1993, in *The Fossil Record 2*), the most recent, comprehensive classification available, now a decade old.

ON THE GENERAL SIGNIFICANCE OF THE MOLTENO

Of all the fossil plant/insect-bearing strata around the world, the Late Triassic Molteno Formaton of the Karoo Basin, South Africa, must rank as one of the most compelling. Resting immediately above the celebrated bone-bearing, Permo-Triassic Beaufort Group—second to none in revealing the story of the transition from reptiles to mammals—lends it further interest. It has not yielded permineralised fruit with exquisitely preserved anatomical structure as in the coal balls of the Euramerican Carboniferous; or the consistent high-quality cuticle of the Yorkshire Jurassic; or a multitude of fully articulated insects as in a number of Cretaceous lagerstatte worldwide; but for sheer potential in revealing the extraordinary richness of the fecund later Triassic, it is apparently without peer. As currently known, it presents the clearest available window onto what may well prove to be the most explosive of all plant radiations, that leading to the acme of gymnosperm diversity and the ecosystems spawning the mammals, dinosaurs and very possibly the stem-angiosperms or flowering plants.

When we made our first collections from the Molteno 35 years ago, there was no reason to suspect any of this. Little Switzerland, with a superb view across to the Jurassic (flood basalts) escarpment of the Natal Drakensberg, wonderfully picturesque itself between sandstone cliff and wet indigenous forest, and with an obviously diverse compression flora, offered a fine debut into the formation. But only as we gradually, almost recklessly, added locality after locality to the collection—and lobbied persistently for more storage space—has the true significance of the Molteno come into focus. Imagine a Michelangelo sculpture gaining progressively in definition as the marble slab is doggedly cleaved and chipped away.

But the most revealing aspect of the Molteno is what has not yet been revealed, what we do not yet know about it, what remains to be uncovered. The 100 sampled plant assemblages (taphocoenoses) with 27 000 catalogued slabs, 43 of which have yielded insect faunas, almost literally represent just the tip of the iceberg. Projections suggest that the 204 species of foliage and 333 species of insect so far identified represent only a fraction of the total *preserved* flora and fauna. The Molteno exposure, the perimeter of a tilted trapezium with dimensions of some 400 by 200 km, will evidently yield hundreds more sites with further searching. According to statistical extrapolations these promise to contain hundreds more species, belonging to many still unknown genera, families and orders of plant. And amongst this exuberant richness may well appear some plants more angiosperm than gymnosperm.

The Molteno, in summary, proves uniquely engaging from a range of interweaving perspectives.

The Triassic explosion. By statistical extrapolation, from *observed* to *preserved* to *existed* species, the Molteno hints at biodiversity figures for insects and plants apparently akin to those in the world today. This strongly contradicts the conventional picture of a '*cone of increasing diversity*' through the past 450 million years. (And. & And. 1995; Anderson *et al.* 1996)

From RNA interference to the Benny effect. With the ever-increasing flood of discoveries, insights and hypotheses in molecular biology over the past decade in particular, we can look at intervals of explosive evolution afresh. Scanning the pages of the most ubiquitous fast-track scientific journals—*Nature*, *Science*, *Scientific American*, *New Scientist*—of just the last year is literally like peering into a new world. We need no longer confine our thinking to conventional Darwinian evolution through random mutation and natural selection. The extraordinary renewal and radiation of terrestrial life through the Triassic can be considered in the new light of our deepening knowledge of the architecture and functioning of chromosomes, genomes and genes. Atavism, Hox genes, stem cells, RNA interference, chromosome shuffling, gene transfer, retroviruses, retroelements, inactive DNA, pre-programming, the Benny effect, individually and together, offer new possibilities for evolution within a period of dramatic radiation. Here we merely cite these concepts; in the sequels to this work we probe their implications with regard to the Molteno flora, the Triassic explosion, biodiversity patterns, gymnosperm classification and the gymnosperm heyday.

Heyday of the gymnosperms. The known Molteno fruit appear to show at least 10 new orders of gymnosperm. A revised global classification (a sequel to this volume) of the division shows a clear peak of gymnosperm diversification in the Late Triassic, with the Molteno as the flagship formation. At the higher taxonomic levels of order and class (basic morphological latitude), the gymnosperms in this early-Mesozoic heyday seem to have outstripped the angiosperms—with only two classes and some 84 orders (pre molecular-based cladistics)—in their recent heyday.

Latitudinal diversity gradient. Wilson (1992), in *The diversity of life*, defined a number of the generally acknowledged laws of biodiversity. One of the most clear-cut was the '*latitudinal diversity gradient*', of which he wrote: '[it is an] *indisputable general feature of life that biodiversity rises towards the tropics*.'

From our work on the Molteno and from an assessment of diversity trends plotted against the Phanerozoic Ice-House/Hot-House climatic curve (Scotese 1998; Scotese *et al.* 1999), we offered the hypothesis (Anderson *et al.* 1999) that this rule might hold, strictly, only for the relatively brief Ice-House intervals occurring intermittently through geological time. One such unordinary interval characterises today's world. How well does the rule hold up during the far longer Hot-House intervals when average global temperatures rose to levels some 20°C hotter? '*In the Late Triassic super-hothouse world at the time of the Molteno, for instance, the definite possibility exists that a partial reversal of today's latitudinal diversity gradient might have held. Energy levels that are now optimal at the equator, might have been too extreme during the Triassic*' (Anderson 1999).

The world's hottest terrestrial hotspot. Current evidence suggests that the intriguing search for this Holy Grail of evolutionary biology might well concentrate on the Late Triassic World—along with the gymnosperm heyday. Further, in marked contrast to the reality of our extant world, it seems to have centred on (southern) temperate rather than tropical latitudes. The uplands bordering the Molteno Floodplain Biome may feasibly lay claim to having supported the world's richest terrestrial hotspot, past or present. We offer this hypothesis as a challenge for debate.

The dawn of the extant world. It was approximately at the time of the Molteno—providing the best available sample of the fecund Late Triassic ecosystems—that the mammals, the dinosaurs, much of the modern spectrum of insect orders (including the super-diversity of the beetles and the abundance of cockroaches), and perhaps the stem-angiosperms, all first evolved. The mammals and flowering plants, both dominant today, seem to have followed a remarkably parallel *ca* 230 million-year life cycle, with the stem group of each having arisen within the great Triassic explosion of life (Anderson 1999).

It is particularly the third of these six themes, *the heyday of the gymnosperms*, that we explore in this volume and its sequels. The emphasis at all taxonomic levels is on biodiversity.

ACKNOWLEDGEMENTS

Many persons have contributed in quite different ways towards making this volume on the Molteno possible. We are grateful, firstly, for the continuing support of the National Botanical Institute, who have fully funded our research since 1975.

Then there are the many farmers on whose lands we have excavated and through whose warm hospitality we have thrived. Since our last volume in 1989, Fred and Linda Terblanche of Aasvoëlberg, Isaac and Else Brummer of Peninsula, and Piet and Sonya De Wet of Lutherskop have, in particular, welcomed us during our repeated invasions from the city. Some 35 field trips have been specifically planned through the 1990s to improve our collections of reproductive material for this volume. Many of these were undertaken with Marijke, friend, and more recently wife, of JMA.

Typing of the text has been done—somewhat fitfully over a good few years as the book steadily expanded—particularly by Daleen Maree, Linda de Kock, Sheryl van Rooyen, and most recently Else van Doornum, Carrie-Ann Greger and Nadine Loots. Nadine has also been largely responsible for scanning in the numerous sketches and for the cover design. Sarie Brink has set the numerous tables and completed the final typesetting. Adela Romanowski, as always, has willingly printed the photographs. Gill Condy and Nicolette Lavoyer (explicitly out from Geneva) have helped with a number of the line drawings. Our daughter, Clara Anderson, and her companion (now husband) Hannes du Plessis, have put the greater part of a month into recreating the 152 photographic plates in Quark Express for electronic publishing. They were hijacked into this endeavour while on a break in South Africa from their architectural careers in London.

A good number of palaeontological colleagues have offered critical comment on aspects of the manuscript at various stages in its lengthy gestation. We particularly thank Chris Cleal, Wolfgang Meier, Andrew Scott, Greg Retallack, Stephen McLoughlan, Raphael Herbst, Sid Ash, Conrad Labandeira and Hallie Sims in this regard. Keith Holmes helped prodigiously in the sprint to the finish. We are deeply grateful to Peter Crane, Director of the Royal Botanic Gardens, Kew, London, for so willingly writing the Foreword.

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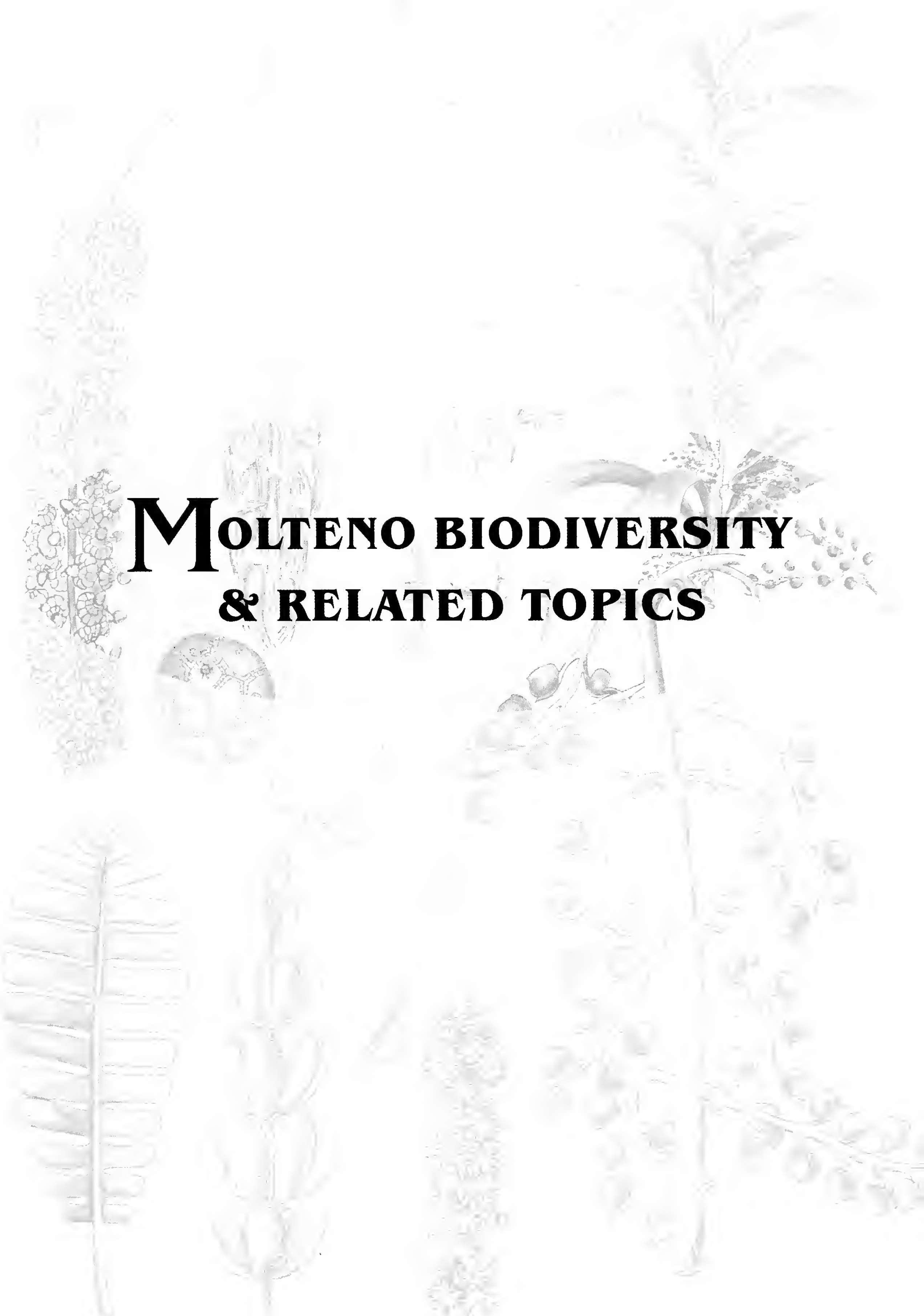
Finally, we wish to acknowledge the Ernest Oppenheimer Memorial Trust for generous sponsorship.



MOLTENO BIODIVERSITY & RELATED TOPICS

1. SAMPLING

Sampling strategy

Particular emphasis is given to the question of sampling in view of its fundamental underpinning of any analysis of biodiversity at successive taxonomic ranks. Two complementary sides to sampling are separately considered.

Extensiveness of sampling: Extensiveness concerns the general comprehensiveness of sampling, i.e. the total number of taphocoenoses (TCs, assemblages) covering the Molteno Fm. The evenness of spread across the geographic, lithostratigraphic, biostratigraphic and ecostratigraphic divisions of the formation is significant. The *frequency* of occurrence of taxa through the Molteno is thus documented.

Intensity of sampling: Intensity concerns the particular comprehensiveness of sampling, i.e. the quantity of material examined (measured in 'man-hours cleaving') and curated (measured in the number of 'catalogued-slabs' and/or 'identifiable vegetative individuals') for each TC. The relative or absolute *abundance* of taxa within each TC is recorded.

The Molteno collection

The data recorded here account only for our own collections housed at the National Botanical Institute, Pretoria (PRE/F/-) and the Bernard Price Institute, Johannesburg (BP/2/-). Other limited collections exist both in South Africa and overseas (see And. & And. 1985).

Collecting programme: 1967–1998 (31 years); 85 field trips.

Extensiveness of sampling: 100 taphocoenoses (assemblages) from 69 localities (areas to 1 km in diameter).

Intensity of sampling: *ca* 27 000 catalogued slabs including *ca* 300 000 identifiable vegetative specimens (individuals).

Geographic grid (hierarchy)	Grid diam.	Vol 1 1983	Vol 2 1989	This vol 2003
subregions	100 km	9	9	10
superlocalities	10 km	36	36	43
localities	1 km	44	48	69
sublocalities	100 m	–	–	80
supersites	10 m	50	57	85
TCs (assemblages)	–	67	75	100
Slabs (approx.)	–	13 400	16 600	27 000

Sampling history, 1967–1998

Sampling bias

In order to assess the comprehensiveness of sampling of the Molteno Fm., four distinct perspectives are considered: geographic, lithostratigraphic, biostratigraphic and ecostratigraphic. How evenly are the 100 Molteno TCs (69 localities, 43 superlocalities) spread throughout the formation?

Geographic. For our Gondwana biogeographic maps we have employed a degree-square grid (And. & And. 1983, 1989), a very convenient scale when plotting distributions at the super-continental level (Map 1, Tabs 2–4). To reflect biogeographic reality, all productive grid squares—those yielding megaplant-bearing strata of Triassic age—should be equally thoroughly sampled, an ideal far from attained as yet.

The 10 degree squares covering the Molteno outcrop are shown on Map 2, and the extensiveness of sampling within each square is recorded in the accompanying Tab. 5.

The number of superlocalities per degree square varies largely according to the thickness and area of outcrop. In degree square Ka 8, for instance, including the thickest Molteno sequences and with as many as 11 productive superlocalities, the potential for discovering further sites is great. The degree square to the West of Ka 1, despite a considerable outcrop (though attenuated lithostratigraphy) and extensive searching, has, as yet, not yielded a single superlocality.

Lithostratigraphic. The lithostratigraphic subdivision of the Molteno into members—each consisting of a fining-upward cycle—has not yet reached stability (Turner 1975; Christie 1981). We follow here the six-member system and nomenclature of Christie (1981). Our sampling varies significantly through the succession.

Cycle	Member	Sampling
6	Loskop	1 TC sampled
5	Tsomo	8 " "
4	Qiba	11 " "
3	Mayaputi	21 " "
2	Indwe	51 " "
1	Bamboesberg	8 " "

Lithostratigraphic sampling bias

The tally of TCs sampled per member is probably a fair reflection of potential. Half of all TCs are seen to occur in the Indwe Member (Cycle 2), while only one is known from the Loskop Member (Cycle 6), i.e. Kenegapoort (Ken 111) topping the list on Tab. 1. The 100 TCs are placed with greater or lesser certainty from oldest (in the Bamboesberg Member) to youngest (in the Loskop Member) within the six-fold sequence.

A comprehensive lithostratigraphic and tectonic account of the Molteno Formation and Karoo Basin can be found in Johnson *et al.* (1997), Turner (1999) and Catuneanu *et al.* (1998).

Biostratigraphic. We provisionally recognise four assemblage zones (Tab. 1, left column) based on the combined megafloral and faunal (insects) components of the formation (And. & And., in prep.). These are not strongly differentiated and may better be recognised as assemblage subzones, especially after systematic cleaning of the ecostratigraphic imprint.

	Assemblage zones (informal)	TCs
4	*Sphenobaiera*/*Scytinoptera*	9
3	*Kannaskoppifolia sp.D*/Ipsviciidae	32
2	*Dicroidium zuberi*/*Moltenocupes*	51
1	*Kanaskoppifolia vincularis*/Permithonidae	8

Biostratigraphic sampling bias

Until further resolved, and for practical purposes, the biostratigraphic zones are taken to coincide loosely with lithostratigraphic boundaries. The imbalance in sampling, as for the members, is probably a reasonable reflection of overall potential.

Ecostratigraphic. Seven primary ecozones (habitats), illustrated on p. 39, are recognised within the Molteno Floodplain Biome (Cairncross *et al.* 1995). These are based on an overall analysis of sedimentary strata, floral associations and insect faunas. They are listed below from most to least complex.

	Ecozones	TCs
1	*Dicroidium* riparian forest (mature)	2
2	" " " (immature)	8
3	" woodland	32
4	*Sphenobaiera* woodland	10
5	*Heidiphyllum* thicket	24
6	*Equisetum* marsh	18
7	Fern/*Kannaskoppia* meadow	4
–	uncertain	3

Ecostratigraphic sampling bias

The sampling is seen to be particularly uneven, with the *Dicroidium* woodland (32 TCs) and *Heidiphyllum* thicket (24 TCs) habitats together yielding over half the total TCs. The mature type of *Dicroidium* riparian forest, with the richest plant assemblages, is represented by only 2 TCs.

The Gondwana & Global Triassic

Gondwana Triassic (levels of sampling)

A measure of the undersampling of Gondwana Triassic strata is documented in And. & And. (1983, pp. 2–27) and And. & And. (1989, pp. 14, 15). By far the fullest succession of megafloras (defined as deriving from a particular formation and basin) is preserved in the series of basins stretching down the eastern tectonic margin of Australia. A full census of all Australian collections made by one of us (JMA) in 1980 provides a quantitative basis for comparison with Molteno sampling. Little collecting has been done in the Australian Triassic since—aside from the Nymboida Flora from the Middle Triassic Basin Creek Formation, Nymboida Sub-basin (Holmes 2000, 2001).

Australia—	28 megafloras, 35 productive degree squares
	203 'localities', *ca* 300 TCs, *ca* 13 000 catalogued slabs
Molteno—	1 megaflora, 10 productive degree squares
	36 localities, 100 TCs, *ca* 30 000 catalogued slabs

Australian Triassic & Molteno megaplant sampling

On a sampling scale of 1 to 5 (reconnaissance to comprehensive), we might rate the Molteno grade 4 (approaching optimal) and the Australian formations overall only 2 (basic) (And. & And. 1989, p.15). Sampling of the Triassic outcrops around the other Gondwana continents remains roughly on a par with Australia.

The near absence elsewhere in Gondwana of most of the reproductive taxa described here from the Molteno will certainly to some significant degree be a reflection of this undersampling.

Global Triassic (levels of sampling)

Triassic floras of the world overall remain highly unequally sampled. Evidence of this is seen, for instance, in the massive imbalances (Anderson *et al.*, in prep., sequel to this work) in the geographic origin of the type species of described and named ovulate (gymnosperm) genera. Of the 58 genera now known from the global Triassic, 17 are based on Molteno specimens, 21 on European Triassic material, and only 13 from all remaining regions of the Triassic world. (A further seven type species are of non-Triassic origin.) It is hardly conceivable that these unequal numbers faithfully reflect phytogeographic or biostratigraphic significance. The European bias is undoubtedly historical, while the Molteno bias reflects, in significant measure, the level of sampling. It is abundantly evident that, although the first ovulate strobilus (Triassic gymnosperms) was described over 170 years ago (1828), we have only begun to scratch the surface. We might safely predict a notable increase in the unearthing and description of new genera, representing new families and orders, in future years.

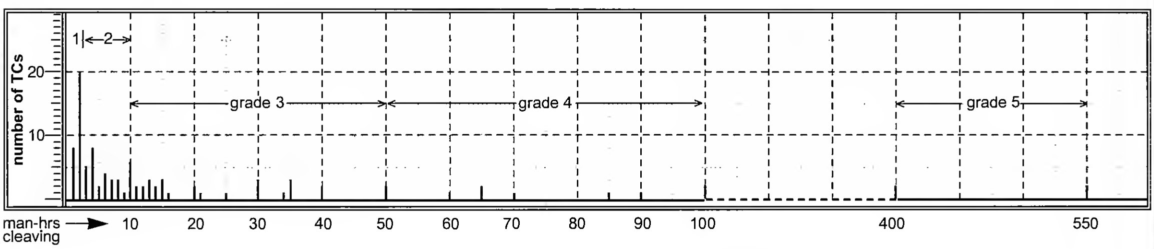


Fig. 4. Sampling intensity of the 100 Molteno assemblages (TCs)

Histogram: following this system of grading, around half the 100 Molteno TCs have been sampled at the reconnaissance to low-intensity level and half at the medium- to top-intensity level

Sampling intensity grade		man-hours cleaving 1–2	3–9	10–49	50–100	>400
Reconnaissance	1	27				
Low intensity	2		27			
Med. intensity	3			33		
High intensity	4				9	
Top intensity	5					4

Sampling intensity grades

Optimal sampling: could aim at grade 3, 4 or 5 intensity depending on the nature and diversity of the assemblage (TC)

Geographic grid (hierarchy)	Upper limit to areas (maximum diameter)	Name code (examples)
Region	1000 km	Saf(Ka)
Subregion	100 km	Ka (from **K**aroo Basin)
Superlocality	10 km	Lit (from **Lit**tle Switzerland)
Locality	1 km	Lit I
Sublocality	100 m	Lit II
Supersite	10 m	Lit III
Site	1 m	—
Subsite	10 cm	—
TC (assemblage)	10 m	Lit III Dic/Hei

The TC (taphocoenosis) is named after the dominant plants occurring in the assemblage; in this case, **Dic**roidium 50% and **Hei**diphyllum 20%

Sampling hierarchy

Spacial occurrence: of fossiliferous strata (see And. & And. (1983, p. 3) for full details)

Tab. 1 MOLTENO 100 TCs

biozones	Molteno cycles	(members)	assemblage (taphocoenosis)	SAMPLING: catalogued slabs: Pre—1989	Post—1989	Total	field trips	days	cleaving (man-hours): site	lab	total	DIVERSITY: ♀ genera	♂ genera	vegetative species: non-gym.	gymno.	total	HABITATS: Dicr. riparian forest (1)	" " (2)	" open woodland	Sphenob. closed "	Heidiphyllum thicket	Equisetum marsh	Fern/Kan. meadow	(uncertain)	DOMINANTS: Dicroidium	Sphenobaiera	Heidiphyllum	horsetails	ferns
4	L	6	Ken 111 Dic cra	32	-	32	1	1	2	-	2	-	-	2	1	3	-	-	✓	-	-	-	-	-	99	-	-	1	3
	TSOMO	5	Nav 111 Equ sp	14	-	14	2	2	2	-	2	-	-	1	-	1	-	-	-	-	-	✓	-	-	-	-	-	100	-
			" Dic odo	60	-	60	2	2	2	-	2	1	-	-	5	5	-	-	✓	-	-	-	-	-	98	-	1	-	-
			Cal 211 Hei elo	21	-	21	1	1	1	1	2	-	-	1	2	3	-	-	-	-	✓	-	-	-	-	-	75	-	20
			111 Equ sp	22	94	116	2	3	8	-	10	-	-	2	-	2	-	-	-	-	-	✓	-	-	-	-	-	99	1
			" Dic/Sph	28	-	28	1	1	2	-	2	-	-	1	5	6	-	-	✓	-	-	-	-	-	50	44	-	-	1
			Bir 211 Sph 2spp	184	-	184	3	3	6	1	7	3	-	2	8	10	-	-	-	✓	-	-	-	-	4	95	3	-	1
			311 Hei/Sph	133	-	133	2	2	2	-	2	5	2	-	7	7	-	-	-	✓	-	-	-	-	14	40	45	-	-
			111 Sph 2spp	1515	412	1927	9	32	430	120	550	6	3	14	16	30	-	-	-	✓	-	-	-	-	1	85	10	20	90
3	QIBA	4/5	Dor 111 Hei elo	24	-	24	2	2	2	-	2	-	-	1	2	3	-	-	-	-	✓	-	-	-	-	-	85	-	5
			Gre 121 "	141	-	141	3	4	7	3	10	1	2	3	4	7	-	-	-	-	✓	-	-	-	3	-	98	20	2
			111 Sph pon	10	-	10	7	6	4	1	5	2	1	-	3	3	-	-	-	-	-	-	-	✓	-	85	10	-	-
			" Equ sp	63	150	213	7	8	20	5	25	1	-	5	5	10	-	-	-	-	-	✓	-	-	2	-	-	97	1
			Boe 111 Lep sto	77	-	77	6	7	7	1	8	1	-	2	5	7	-	-	-	-	-	-	-	✓	5	-	7	-	2
			" Equ sp	37	-	35	5	6	11	-	11	-	-	1	-	1	-	-	-	-	-	✓	-	-	-	-	-	100	-
			" Dic/Hei	98	-	98	6	7	7	1	8	1	-	-	8	8	-	-	✓	-	-	-	-	-	57	-	42	-	-
			112 Dic cor	179	-	179	2	2	4	2	6	2	2	1	11	12	-	-	✓	-	-	-	-	-	99	-	14	4	-
			Cyp 111 Dic cra	38	324	362	4	6	30	70	100	3	1	4	8	12	-	-	✓	-	-	-	-	-	75	-	24	-	4
			" Hei elo	8	-	8	1	1	2	-	2	-	-	-	1	1	-	-	-	-	✓	-	-	-	-	-	100	-	-
			Mol 111 Sph pon	80	15	95	4	4	6	-	6	2	-	-	4	4	-	-	-	✓	-	-	-	-	12	99	-	-	-
	MAYAPUTI	3	Kan 112 Hei elo	48	97	145	2	3	15	-	15	1	2	4	9	13	-	-	-	-	✓	-	-	-	1	-	98	6	7
			111 Ast spA	41	324	365	4	7	22	8	30	2	-	4	3	7	-	-	-	-	-	-	✓	-	-	-	10	22	63
			Tel 111 Hei elo	203	378	581	7	10	60	30	90	3	5	7	13	20	-	-	-	-	✓	-	-	-	6	-	89	48	58
			Kom 111 Sph/Dic	124	44	168	3	4	10	-	10	1	1	3	4	7	-	-	✓	-	-	-	✓	-	39	60	-	15	1
			Vin 111 Dic odo	166	-	166	2	2	10	-	10	-	1	2	8	10	-	-	✓	-	-	-	-	-	70	4	28	-	2
			Ela 111 "	235	-	235	1	1	8	2	10	4	2	1	8	9	-	-	✓	-	-	-	-	-	87	1	7	-	4
			Kra 311 "	103	56	159	2	2	11	2	13	1	2	-	3	3	-	-	✓	-	-	-	-	-	99	-	5	-	-
			211 Equ sp	27	172	199	2	3	4	-	4	-	-	1	-	1	-	-	-	-	-	✓	-	-	-	-	-	100	-
			221 beetles	-	-	13	1	1	2	-	2	-	-	2	1	3	-	-	-	-	-	-	-	✓	50	-	-	50	1
			111 Dic odo	380	-	380	2	2	11	9	20	2	2	3	6	9	-	-	✓	-	-	-	-	-	90	1	-	-	4
			Lut 111 Hei/Dic	23	-	23	1	1	2	-	2	1	-	1	2	3	-	-	-	-	✓	-	-	-	40	-	50	10	-
			511 Hei elo	-	26	26	1	1	2	-	2	1	-	1	2	3	-	-	-	-	✓	-	-	-	-	-	80	-	1
			4112 Hei/Dic	-	60	60	1	2	2	-	2	1	-	-	2	2	-	-	-	-	✓	-	-	-	50	-	50	-	-
			4111 Equ sp	-	57	57	1	2	2	-	2	-	-	1	-	1	-	-	-	-	-	✓	-	-	-	-	-	100	-
			311 Hei elo	-	589	589	3	8	46	4	50	6	5	4	14	18	-	-	-	-	✓	-	-	-	58	29	99	30	3
			221 Equ sp	-	16	16	1	1	1	-	1	-	-	1	1	2	-	-	-	-	-	✓	-	-	1	-	-	99	-
			211 "	-	15	15	1	1	1	-	1	-	-	1	4	5	-	-	-	-	-	✓	-	-	-	10	-	80	2
			Tin 121 Sph 2spp	33	-	33	2	2	5	-	5	3	1	1	8	9	-	-	-	✓	-	-	-	-	1	95	4	1	-
			111 Sch sp	88	-	88	2	2	3	-	3	-	-	2	1	3	-	-	-	-	-	✓	-	-	-	-	10	89	-
			131 Hei/Ast	18	-	18	2	2	3	-	3	-	-	2	1	3	-	-	-	-	✓	-	-	-	-	-	50	10	40
		2/3	Wal 111 Dic odo	339	-	339	3	3	40	10	50	2	1	-	11	11	-	-	-	✓	-	-	-	-	92	3	-	-	-
2	INDWE (2)	f	Kon 223 "	-	104	104	2	3	5	2	7	-	-	5	10	15	-	-	✓	-	-	-	-	-	80	1	1	-	1
			222 "	305	144	449	4	5	13	17	40	5	6	8	14	22	-	-	✓	-	-	-	-	-	87	10	-	1	1
			221 Ast 2spp	[276	[117	[393	[8	[8	16	-	16	-	-	7	5	12	-	-	-	-	-	-	✓	-	-	-	-	20	52
			211						14	-	14	-	-	6	5	11	-	-	-	-	-	-	✓	-	-	-	-	20	52
			211 Hei elo	22	-	22	1	1	1	-	1	-	-	-	2	2	-	-	-	-	✓	-	-	-	5	-	95	-	-
			111 Dic odo	285	-	285	4	4	30	4	34	2	1	3	16	19	-	-	✓	-	-	-	-	-	78	5	7	1	12
			" Sch sp	12	-	12	1	1	1	-	1	-	-	1	1	2	-	-	-	-	-	✓	-	-	-	-	10	90	-
			" Hei elo	55	-	55	2	2	4	-	4	2	-	1	3	4	-	-	-	-	✓	-	-	-	3	-	84	10	-
			Pen 321 Dic/Ris	-	408	408	3	5	22	13	35	3	3	4	14	18	-	-	✓	-	-	-	-	-	51	5	1	32	5
			211 Dic/Equ	-	104	104	2	2	4	-	4	-	-	4	5	9	-	-	✓	-	-	-	-	-	50	-	2	45	2
			221 "	-	200	200	2	2	5	-	5	-	-	4	6	10	-	-	-	-	-	✓	-	-	40	-	-	40	20
			511 Equ sp	-	152	152	1	1	6	-	6	-	-	2	2	4	-	-	-	-	-	✓	-	-	2	-	-	98	-
			421 Dic odo	-	61	61	2	3	7	-	7	-	-	1	8	9	-	-	✓	-	-	-	-	-	89	4	4	5	-
			431 Dic/Equ	-	53	53	1	1	1	-	1	-	-	4	5	9	-	-	✓	-	-	-	-	-	40	-	5	40	-
			311 Hei elo	-	155	155	4	11	32	3	35	3	1	5	6	11	-	-	-	-	✓	-	-	-	25	-	75	5	11
			411 "	-	204	204	4	11	60	10	70	3	1	6	5	11	-	-	-	-	✓	-	-	-	13	-	94	2	3
			Kle 111 Equ sp	35	-	35	3	3	4	-	4	-	1	1	1	2	-	-	-	-	-	✓	-	-	-	-	1	99	-
			" Hei elo	15	-	15	3	3	15	-	15	1	-	1	1	2	-	-	-	-	✓	-	-	-	-	-	90	10	-
			" Hei/Dic	288	-	288	3	3	9	-	9	3	-	-	9	9	-	-	-	-	✓	-	-	-	45	8	49	-	-
		e	211 Sph pon	14	-	14	2	2	1	-	1	-	-	-	1	1	-	-	-	✓	-	-	-	-	-	100	-	-	-
			Kul 111 "	10	-	10	1	1	1	-	1	-	-	2	2	4	-	-	-	✓	-	-	-	-	-	99	-	2	1
			Kap 111 Dic/Ris	-	1310	1310	5	10	40	25	65	6	3	5	14	19	-	✓	-	-	-	-	-	-	50	20	25	10	4
		d	Vin 211 Sch sp	50	-	50	2	2	3	-	3	-	-	1	-	1	-	-	-	-	-	✓	-	-	-	-	-	100	-
			Ela 112 Equ sp	25	128	153	2	2	11	3	14	-	-	2	1	3	-	-	-	-	-	✓	-	-	1	-	-	95	4
			" Dic/Hei	41	-	41	1	2	4	-	4	-	-	1	2	3	-	-	-	-	✓	-	-	-	60	-	30	10	-
			Nuw 111 Equ sp	22	266	288	5	5	15	-	15	-	-	2	-	2	-	-	-	-	-	✓	-	-	-	-	-	99	-
			" Dic zub	138	-	138	3	3	20	-	21	2	1	1	8	9	-	-	✓	-	-	-	-	-	70	30	-	-	4
			211 Dic 2spp	119	-	119	1	1	6	-	6	1	-	-	6	6	-	-	✓	-	-	-	-	-	99	3	1	-	-
			Win 111 Hei elo	64	-	64	2	2	18	2	20	1	1	5	6	11	-	-	-	-	✓	-	-	-	10	-	79	2	3
		c	Mor 111 Dic zub	50	-	50	2	2	12	-	12	-	-	1	3	4	-	-	✓	-	-	-	-	-	99	-	-	-	1
			" Dic odo	214	-	214	2	2	12	-	12	1	2	1	3	4	-	-	✓	-	-	-	-	-	98	-	-	-	-
			Qua 111 "	140	-	140	1	1	6	2	8	1	-	-	4	4	-	-	✓	-	-	-	-	-	40	20	20	-	-
			Mak 111 "	146	-	146	1	1	10	-	10	-	-	1	4	5	-	-	✓	-	-	-	-	-	90	1	-	-	-
			Maz 111 Dic cra	462	-	462	2	3	26	4	30	1	2	3	13	16	-	✓	-	-	-	-	-	-	74	12	5	5	3
			211 Hei/Dic	919	168	1087	4	7	50	35	85	5	3	4	15	19	-	✓	-	-	-	-	-	-	64	1	32	7	4
		b	Moo 111 Dic zub	-	78	78	1	2	5	-	5	-	-	-	5	5	-	-	✓	-	-	-	-	-	99	5	-	-	-
			Hla 111 Equ sp	14	-	14	1	1	1	-	1	-	-	1	1	2	-	-	-	-	-	✓	-	-	1	-	-	99	-
			211 Dic 3spp	157	-	157	3	3	3	1	4	2	1	4	13	17	-	✓	-	-	-	-	-	-	85	7	-	10	1
			212 "	217	-	217	2	3	9	2	11	2	1	2	18	20	-	✓	-	-	-	-	-	-	91	7	-	1	6
			213 Dic elo	902	-	902	3	7	60	-	60	4	2	15	28	43	-	✓	-	-	-	-	-	-	89	49	1	11	32
			Umk 111 Dic 2spp	3203	389	3592	10	20	125	275	400	10	5	29	46	75	✓	-	-	-	-	-	-	-	69	5	7	2	1
			Cha 111 Dic odo	-	38	38	1	1	2	-	2	-	-	-	1	1	-	-	✓	-	-	-	-	-	100	-	-	-	-
			211 Dic dub	-	12	12	1	1	2	-	2	-	-	1	1	2	-	-	✓	-	-	-	-	-	80	-	-	20	-
			Inj 111 Dic odo	-	33	33	1	1	2	-	2	-	-	1	3	4	-	-	✓	-	-	-	-	-	100	-	-	-	1
			211 Dic dub	-	21	21	1	1	2	-	2	-	-	-	4	4	-	-	✓	-	-	-	-	-	90	-	10	-	-
			San 111 Dic cra	303	-	303	3	3	24	6	30	5	3	3	16	19	-	✓	-	-	-	-	-	-	90	-	5	2	1
			Mng 111 Dic 2spp	68	-	68	1	1	2	-	2	-	-	-	8	8	-	-	✓	-	-	-	-	-	93	6	6	-	-
			Qac 111 Hei/Dic	112	-	112	2	2	4	-	4	1	2	2	3	5	-	-	-	-	✓	-	-	-	50	8	50	-	2
			Mat 111 Dic dub	1082	-	1082	5	7	47	18	65	5	4	10	18	28	-	✓	-	-	-	-	-	-	89	18	4	20	7
		a	Gol 111 "	-	108	108	3	3	13	-	13	1	1	-	2	2	-	-	✓	-	-	-	-	-	99	-	-	-	-
			Lit 111 Dic/Hei	1980	193	2173	19	33	250	300	550	7	7	6	32	38	✓	-	-	-	-	-	-	-	50	1	23	10	10
1	BAMBOESBERG	1	Aas 611 Hei elo	-	47	47	1	1	3	-	3	1	-	1	2	3	-	-	-	-	✓	-	-	-	-	-	80	-	1
			111 "	61	230	291	3	3	12	28	40	1	2	7	6	13	-	-	-	-	✓	-	-	-	7	1	77	10	20
			211 "	-	154	154	4	4	8	27	35	1	1	3	4	7	-	-	-	-	✓	-	-	-	-	-	99	-	2
			311 "	-	528	528	11	14	15	125	140	1	2	4	7	11	-	-	-	-	✓	-	-	-	15	9	99	-	2
			411 Dic/Sph	-	2176	2176	11	40	325	187	512	12	8	8	22	30	-	-	-	✓	-	-	-	-	60	30	1	75	24
			511 Dic elo	-	27	27	1	1	2	-	2	-	-	-	11	11	-	-	-	✓	-	-	-	-	50	20	20	-	-
			Ask 111 Equ sp	161	205	366	2	3	12	2	14	1	1	7	5	12	-	-	-	-	-	✓	-	-	21	1	-	50	9
			Bam 111 Dic dub	52	-	52	2	2	3	-	3	-	-	-	5	5	-	-	✓	-	-	-	-	-	98	-	1	-	-
			Total indivs (approx.)	16,600	10,600	27,200											2	8	32	10	24	18	4	3					

Sampling

Sampling the primary habitats (Molteno)

***Dicroidium* riparian forest (mature, type 1)**—Although this habitat is the richest with regard to floral diversity, with Lit 111 (Little Switzerland) yielding 38 vegetative species and Umk 111 (Umkomaas Valley) 75 species, it remains the least extensively sampled (with only two TCs). These sites are confined to the more northerly outcrop area of the Molteno where the formation thins rapidly and the potential for finding further TCs is relatively low. It is, however, in this mature vegetation, interpreted as growing on the earlier, erosive, Triassic landsurface—with the lowest Indwe Sandstones of the Molteno unconformably overlying the Lower to early-Middle Triassic Beaufort beds—where the greatest potential evidently lies for significant new taxonomic finds. Umk 111, for instance, has yielded three of the nine ovulate genera recorded, as yet, from only a single TC.

***Dicroidium* riparian forest (immature, type 2)**—This second category of riverine forest (with eight TCs), interpreted to have never reached great maturity owing to the shifting nature of the braided rivers, is relatively rich in both vegetative species and ovulate genera. The TCs are particularly varied and mixed in character in that they were deposited under very different conditions on either side of the narrow forested levees: either in near-bank channels of the braided river or on the proximal floodplain associated with crevasse splays. Sampling of this habitat is not particularly comprehensive and further focus on it will surely prove productive.

***Dicroidium* open woodland**—By area, this vegetation type probably occupied a greater part of the Molteno Biome than any other. It has been well sampled from 32 TCs. The floral diversity was relatively low as is reflected in the low to medium diversity of the preserved assemblages. *Umkomasia* and *Peltaspermum* are the most frequently encountered ovulate genera, while other forms are few and far between. There is evidently relatively little new to be discovered.

***Sphenobaiera* closed woodland**—It is these closed woodlands fringing the lakes of the floodplain, along with the two grades of *Dicroidium* riparian forest, that were the richest vegetation types of the Molteno Biome. They have yielded the greatest diversity of ovulate genera. With only 10 TCs, this habitat remains undersampled. The discovery of further TCs of the quality of Bir 111 and Aas 411 will very likely bring a good number of new fruit genera to light. It is pertinent that Aas 411 has produced the record diversity of ovulate genera for the Molteno (13 in all) and that three of these are unique to the site.

***Heidiphyllum* thicket**—These low-diversity *Heidiphyllum* (conifer)-dominated assemblages have been particularly well sampled from 24 TCs. They generally yield only two or three genera of ovulate structure, most notably *Telemachus* (affiliated with *Heidiphyllum*), *Dordrechtites* and *Kannaskoppia*. Other ovulate genera are rarely encountered and further sampling of this habitat is unlikely to unearth significant new reproductive finds.

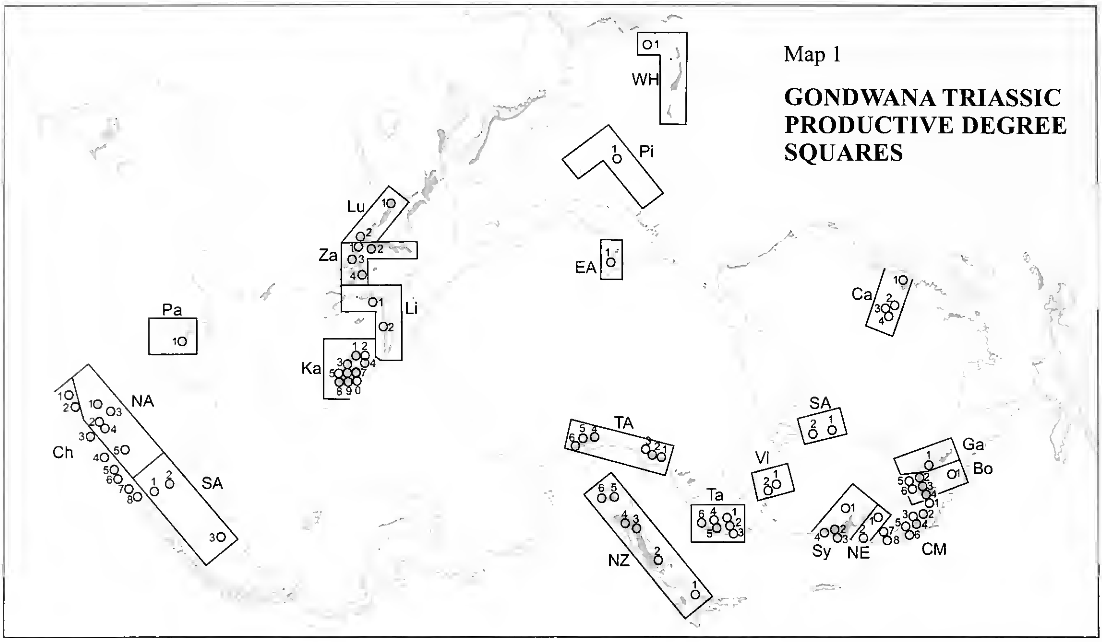
***Equisetum* marsh**—This vegetation type is often encountered in the Molteno and, with 18 TCs sampled, has been well covered. The original communities were presumably mostly monospecific and the allochthonous gymnospermous elements in the fossil assemblages are rare: only two TCs of this category have yielded ovulate or microsporangiate structures.

Fern/*Kannaskoppia* meadow—With only four TCs, these meadows of the braid-river sandbanks remain undersampled. This is due to the nature of the deposits: generally coarse, poorly bedded sediments reflecting rapid burial under turbulent flow conditions. Kan 111 and Kom 111, representing this habitat, are the only TCs from the Molteno (aside from single *Hamshawvia*/*Sphenobaiera* and *Stachyopitys*/*Sphenobaiera* specimens from Aas 411 and Maz 211 respectively; p. 16) that have yielded gymnospermous shoots with fruit and foliage attached (see *Kannaskoppia*/*Kannaskoppifolia*, pp. 286–297). We anticipate that further sampling of this vegetation type may well yield important additional finds of fruit and foliage in organic connection.

Annotated notes for TAB. 1.

Tab. 1. Sampling the Molteno Fm., 100 taphocoenoses (TCs)

Geographic: see Map 2 and Tab. 5
Lithostratigraphic: the full set of 100 sampled Molteno TCs is included in lithostratigraphic sequence according to the six recognised sedimentary cycles (members); L=Loskop member (Cycle 6)
Biostratigraphic: the four provisionally defined assemblage subzones (manuscript in prep.) coincide approximately with the lithostratigraphic boundaries as shown
Ecostratigraphic (habitats): it is indicated, for each of the 100 TCs, which of the seven primary habitats (ecozones) characterising the Molteno Biome is represented
Sampling: 27 200 catalogued slabs have been collected to date; 16 600 prior to our last monograph on the Molteno (And. & And. 1989) and 10 600 subsequently
Diversity: the generic diversity of gymnospermous fruit and species diversity of all vegetative taxa are recorded
Dominants: to provide the essential character of each TC, the dominant gymnospermous genera and non-gymnospermous groups are given
Bold = % estimate made at site
Mild = individuals in curated collection (where < 1%)



Updated from And. & And. (1983 & 1989)

Tab. 2 GONDWANA TRIASSIC, PRODUCTIVE DEGREE SQUARES

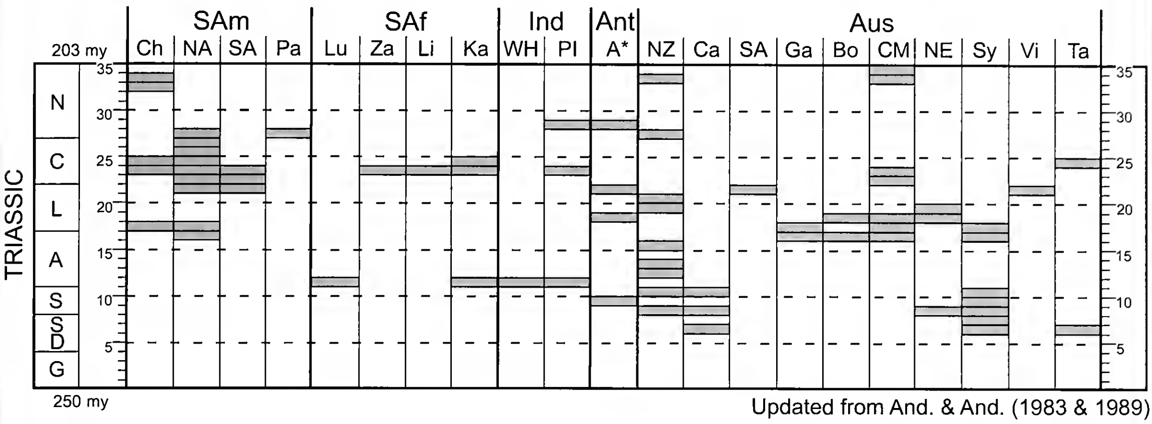
SUPERREGION (continent) / REGION (basin) / Subregion (° square)	Degree square Lat.	Degree square Long.	Quantity	Quality	Cuticle	Publ. cover	Biozones	Localities
SOUTH AMERICA (SAm)								
CHILE (Ch)								
1 Copiapo	27	70	3	3	–	2	1	3
2 Alto del Carmen	29	71	•	•	–	1	1	1
3 Los Vilos	32	72	2	2	–	2	1	2
4 Curicó	34	72	•	•	–	1	1	1
5 Pocillas	36	73	•	•	–	1	1	1
6 Concepción	37	73	3	3	–	2	2	2
7 Temuco	38	73	•	•	–	1	1	2
8 Valdivia	39	73	•	•	–	1	1	1
N. ARGENTINA (NA)								
1 Ischigualasto	29	69	3	3	3	2	3	13
2 Barreal	31	70	4	4	2	4	2	6
3 Marayes	31	68	2	3	–	2	1	1
4 Cacheuta	32	70	4	4	3	3	3	10
5 Llantenes	35	69	3	3	–	3	2	2
S. ARGENTINA (SA)								
1 Paso Flores	40	72	2	3	–	2	1	1
2 Los Menucos	40	69	1	2	–	1	1	1
3 El Tranquilo	47	70	2	3	–	2	1	1
PARANA BASIN (Pa)								
1 Santa Maria	29	54	2	3	–	2	1	1
SOUTHERN AFRICA (SAf)								
LUANGWA VALLEY (Lu)								
1 N. Luangwa V.	10	32	1	1	–	1	1	•
2 W. Luano V.	14	29	•	•	–	1	1	•
ZAMBEZI VALLEY (Za)								
1 Kafue V.	15	28	•	•	–	1	1	•
2 Urungwe	16	30	1	1	–	1	1	1
3 Lake Kariba	17	27	3	3	–	2	1	8
4 Gwelo	19	29	2	2	–	2	1	1
LIMPOPO VALLEY (Li)								
1 Soutpansberg	22	30	1	1	–	1	1	1
2 Komatipoort Cf.	25	31	1	1	–	1	1	1
KAROO BASIN (Ka)								
1 Bethlehem	28	28	1	3	5	2	1	1
2 Bergville	28	29	5	5	5	4	1	1
3 Maseru	29	27	5	5	3	4	1	4
4 Underberg	29	29	5	5	3	4	1	9
5 Aliwal North	30	26	5	4	–	4	2	13
6 Zastron	30	27	4	4	–	4	1	2
7 Matatiele	30	28	4	4	–	4	1	5
8 Molteno	31	26	5	4	–	4	1	19
9 Elliot	31	27	4	4	–	4	2	14
10 Maclear	31	28	4	4	–	4	1	1
INDIA (Ind)								
W. HIMALAYAS (WH)								
1 Salt Range (W)	33	71	2	2	–	2	1	1
PENINSULA INDIA (Pi)								
1 S. Rewa/Tiki	24	81	3	3	3	3	3	7
ANTARCTICA (Ant)								
TRANSANTARCTIC MTS. (TA)								
1 Allan Nunataks	76	155	3	4	–	2	1	3
2 Taylor Glacier	77	155	3	4	3	1	2	9
3 Portal Mt.	78	155	2	3	–	1	1	1
4 Beardmore Gl.	84	160	•	•	•	1	2	3
5 Mt. Bumstead	85	170	2	4	–	2	1	1
6 Shackleton Gl.	85	180	2	4	–	1	1	1
EASTERN ANTARCTICA (EA)								
1 Prince Charles Mts	70	68	3	3	5	3	1	3
AUSTRALASIA (Aus)								
NEW ZEALAND (NZ)								
1 SW Auckland	38	174	1	1	–	4	1	1
2 Nelson Syncline	41	173	1	1	–	4	2	3
3 Mt. Potts	43	170	3	3	–	4	1	1
4 Benmore Dam	44	170	3	3	–	4	1	3
5 Southland Syncl. (NW)	45	168	2	1	–	4	5	10
6 Southland Syncl. (SE)	46	169	2	1	–	4	2	7
CANNING BASIN (Ca)								
1 Derby	17	123	2	3	2	2	1	2
2 Mt. Erskine	19	126	2	3	–	1	2	4
3 Mt. Ernest	20	126	2	2	–	1	2	8
4 Gregory Lake	20	127	2	2	–	1	2	3
SOUTH AUSTRALIA (SA)								
1 Leigh Creek Cf.	30	138	3	3	5	3	1	1
2 Springfield Cf.	32	138	3	3	–	3	1	1
GALILEE BASIN (Ga)								
1 Lennox	22	146	1	2	–	1	1	3
BOWEN BASIN (Bo)								
1 Carborough	21	148	1	2	–	1	1	1
2 Springsure Shelf	24	147	1	2	–	1	1	1
3 Springsure Anticl.	24	148	1	2	–	1	1	1
4 Dawson Range	24	149	1	2	–	1	1	1
5 Carnarvon Range	25	148	1	2	–	1	1	1
6 Taroom	25	149	1	2	–	1	1	3
CLARENCE/MORETON BASIN (CM)								
1 Callide Cf.	24	150	2	4	5	2	1	1
2 Gayndah	25	151	1	3	–	1	1	2
3 Tarong	26	151	2	2	2	1	1	5
4 Esk Trough (N)	26	152	3	4	–	2	1	17
5 Ipswich/Esk	27	152	5	5	5	4	3	54
6 Brisbane	27	153	4	5	4	3	2	14
7 Nymboida	29	152	4	5	–	3	1	4
8 Red Cliff	29	153	2	4	3	2	1	2
NEW ENGLAND FOLDBELT (NE)								
1 Delungra	39	150	2	3	1	3	1	2
2 Lorne Basin	31	152	3	3	–	4	1	4
SYDNEY BASIN (Sy)								
1 Dubbo	32	148	3	4	–	2	1	2
2 Blue Mts.	33	150	2	3	–	3	2	5
3 Sydney	33	151	4	4	3	3	2	23
4 Picton	34	150	2	3	–	2	2	4
VICTORIA (Vi)								
1 Yandolt Hill	36	143	1	1	–	2	1	1
2 Bald Hill	37	144	1	1	–	2	1	1
TASMANIA (Ta)								
1 Poatina	41	146	•	•	•	1	1	1
2 Ben Lomond	41	147	3	4	3	2	1	2
3 NE coast	41	148	3	4	3	2	1	17
4 Derwent Valley	42	146	3	4	3	2	1	2
5 Hobart	42	147	3	4	3	2	2	8
6 South Cape	43	146	1	3	3	2	1	2

22 regions
85 productive degree squares (subregions)
94 biozones (megafloras)
391 localities (69 Molteno, 322 non-Molteno)

– nil
• no information

Sampling

Tab. 3. GONDWANA TRIASSIC, STRATIGRAPHIC OCCURRENCE OF MEGAPLANTS



Updated from And. & And. (1983 & 1989)

Tab. 4. THE MEGAPLANT-BEARING FORMATIONS OF THE GONDWANA TRIASSIC

SOUTH AMERICA

Chile (Ch)
34 La Ternera
" El Puquen
" Gomero
" Tralcan
33 Gomero
" Tralcan
25 Quilacoya
24 Quilacoya
18 (Alto Del Carmen)

N. Argentina (NA)
28 Ischigualasto
" Q de la Mina
27 C. de Piedra
25 L. Carrizal
" Cacheuta
24 Panul
" Potrerillos
" Llantenes
23 Los Rastros
" Cortaderita
" Chihuiu (U)
22 Ischichuca
" Barreal
18 Las Cabras (M/U)
17 Las Cabras (L)

S. Argentina (SA)
24 Paso Flores
23 El Tranquilo
22 Los Menucos

Parana Basin (Pa)
28 Santa Maria

SOUTHERN AFRICA

Luangwa Valley (Lu)
24 'U. Grit'
12 Ntawere

Zambezi Valley (Za)
24 'Flags'

Limpopo Valley (Li)
24 (Molteno)

Karoo Basin (Ka)
25 Molteno
24 Molteno
12 Burgersdrop

INDIA

W. Himalayas (WH)
12 Landa

Peninsular India (PI)
29 Tiki
24 Chicharia
12 Parsora

ANTARCTICA (TA, EA)

Transantarctic Mts.
22 Falla
" Lashly C
19 Fremouw
10 Lashly A

Eastern Antarctica
29 Flagstone Bench

AUSTRALASIA

New Zealand (NZ)
34 (Southland)
28 (Southland)
21 Tank Gully
" Black Jacks
" Long Guily
20,16,14 (Southland)
13,11,9 (")

Canning Basin (Ca)
11 Culvida
9 Erskine
7 Blina

South Australia (SA)
22 Leigh Creek
" Springfield

Galilee Basin (Ga)
18 Moolayember
17 Clematis

Bowen Basin (Bo)
19 Moolayember
17 Clematis

Clarence/Moreton Basin
35 Raceview
34 Aberdare
24 Callide
" Ipswich (U)
23 Tarong
" Ipswich (L)
" Tingalpa
" Red Cliff
19 Esk
" Nymboida
18 Neara
17 Bryden

New England Foldbelt
20 Gragin
19 Gunnee
9 Camden Head

Sydney Basin (Sy)
18 Benolong
" Wianamatta
17 Hawkesbury
11 Burralow
" Gosford (U)
" Newport (U)
10 Newport (M)
9 Garie
" Newport (L)
8 Banks Wall
" Gosford (L)
" Bald Hill
7 Patonga
" Bulgo

Victoria (Vi)
22 Yandoit
" Bald Hill

Tasmania (Ta)
25 Brady
" New Town
7 Knocklofty

Updated from And. & And. (1989)

Explanatory notes

(a) The table provides the base for showing the stratigraphic distribution of each genus.

(b) In the interest of ready comparison with our previous Molteno monographs (And. & And. 1983, 1989), no attempt has been made to update correlations or to introduce the latest standard time scale. A series of fully annotated correlation charts appears in And. & And. (1983).

(c) N—Norian L—Ladinian S—Spathian D—Dienerian
C—Carnian A—Anisian S—Smithian G—Griesbachian

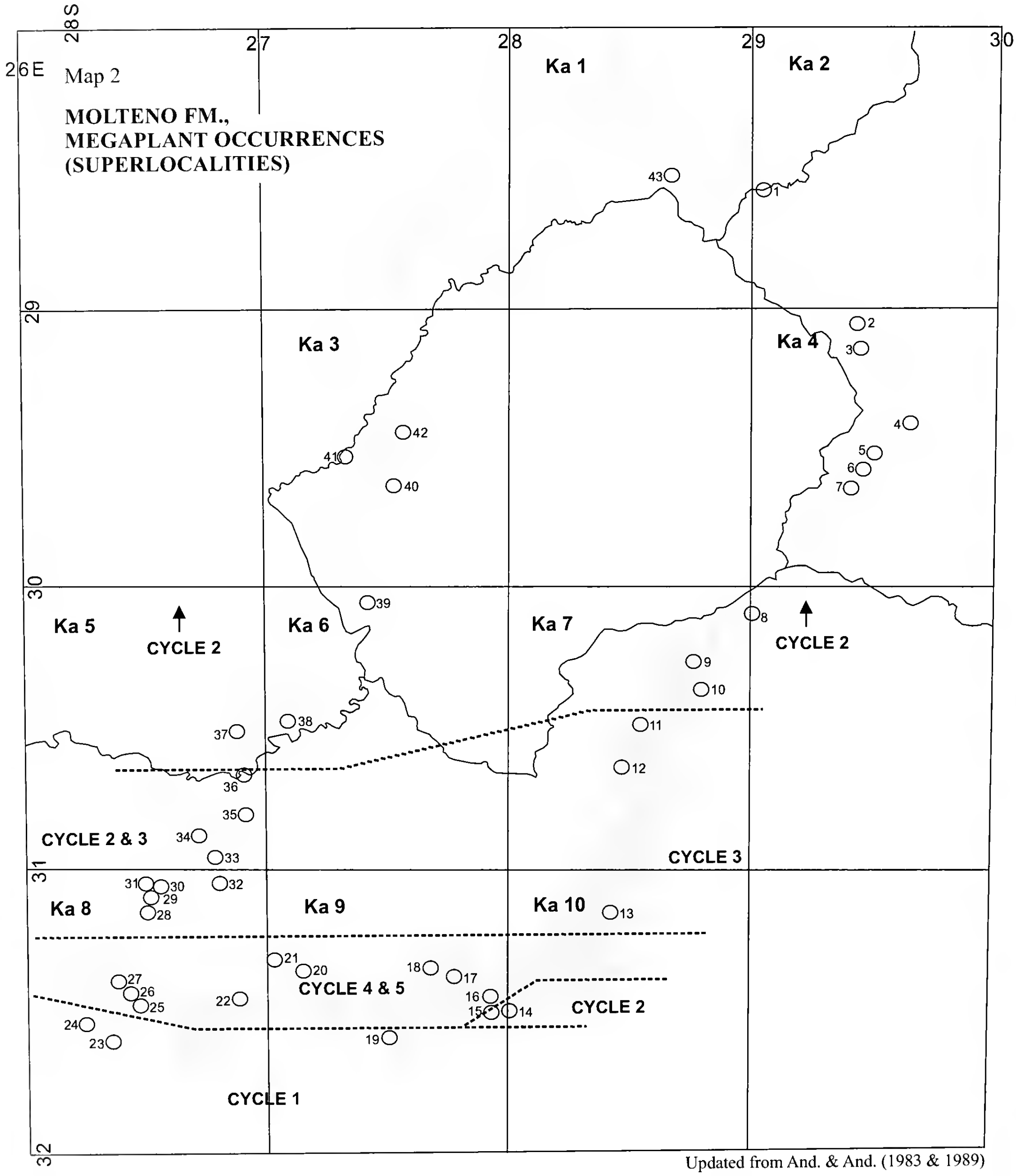
(d) The 35 units into which the Triassic is subdivided represent the international standard ammonite biozones. In that the duration of the Triassic Period (see p. 45) was about 47 million years (250–203 my), each unit or zone represents about 1,3 million years.

(e) The 22 Gondwana regions ('basins') yielding Triassic megaplants are each allotted a single column. Antarctica is an exception: Eastern Antarctica (Flagstone Bench Fm. of the Prince Charles Mts.) has been newly incorporated in the table but not given a separate column—A* = TA + EA.

(f) The coloured bars represent megaplant-bearing strata. For convenience each productive formation (or other sets of beds) is taken to coincide in duration with a particular ammonite biozone.

(g) A bar may represent a single productive formation or a number of correlative formations in adjacent subregions (degree squares). In a few instances (e.g. Molteno, Ipswich) a formation is represented by 2 bars.

(h) The productive 'formations' are listed youngest to oldest for each region and numbered according to the ammonite zonation.



Updated from And. & And. (1983 & 1989)

Sampling

Degree square		Superlocality	Super-site	Assem-blage	Supersite (informal)
Ka 2	1	Little Switzerland	Lit 111	Dic/Hei	–
	2	Champagne Castle	Cha 111	Dic odo	Champagne Hotel
	"	" "	" 211	Dic dub	Wonder Valley
	3	Injasuti Valley	Inj 111	Dic odo	Injasuti Camp
	"	" "	" 211	Dic dub	Forest Patch
	4	Mooi River	Moo 111	Dic zub	–
Ka 4	5	Hlatimbe Valley	Hla 111	Equ sp	Homestead Boulder
	"	" "	" 211	Dic 3spp	Tom's Outcrop
	"	" "	" 212	" "	Eddie's Outcrop
	"	" "	" 213	Dic elo	*Batiopteris* Corner
	6	Umkomaas Valley	Umk 111	Dic 2spp	Waterfall Locality
	7	Sani Pass	San 111	Dic cra	–
	8	Mngeni Valley	Mng 111	Dic 2spp	–
	9	Qachasnek	Qac 111	Hei/Dic	–
	10	Matatiele	Mat 111	Dic dub	–
Ka 7	11	Kenegapoort	Ken 111	Dic cra	–
	12	Tina Bridge	Tin 111	Sch sp	Tina Road
	"	" "	" 121	Sph 2spp	Tina Quarry
	"	" "	" 131	Hei/Ast	Tina Stream
Ka 10	13	Waldeck	Wal 111	Dic odo	" "
	14	Konings Kroon	Kon 111	Dic odo	Du Toit Chert
	"	" "	" "	Sch sp	" "
	"	" "	" "	Hei elo	" "
	"	" "	" 211	Ast 2spp	Rooipoort Donga
	"	" "	" "	Hei elo	" "
	"	" "	" 221	Ast 2spp	" Stream
	"	" "	" 222	Dic odo	Rosy Chert
	"	" "	" 223	" "	Keith Chert
	15	Peninsula	Pen 321	Dic/Ris	*Rissika* Chert
	"	"	" 211	Dic/Equ	Isaac Chert
	"	"	" 221	" "	Volker Chert
	"	"	" 511	Equ sp	Mudpatch Chert
	"	"	" 421	Dic odo	360° Chert
Ka 9	"	"	" 431	Dic/Equ	180° Chert
	"	"	" 311	Hei elo	Campsite Quarry
	"	"	" 411	" "	Lunchspot
	16	Kannaskop	Kan 111	Ast spA	*Kannaskoppia* Siltstone
	"	"	" 112	Hei elo	Upper End
	17	Navar	Nav 111	Equ sp	Elliot Quarry
	"	"	"	Dic odo	" "
	18	Cala Road	Cal 111	Equ sp	Cala Cutting
	"	" "	" "	Dic/Sph	" "
	"	" "	" 211	Hei elo	Cala Bolders
	19	Askeaton	Ask 111	Equ sp	–
	20	Greenvale	Gre 111	Sph pon	*Equisetum* cutting
	"	"	" "	Equ sp	" "
	"	"	" 121	Hei elo	*Telemachus* Shale
	21	Dordrecht	Dor 111	Hei elo	–

Degree square		Superlocality	Super-site	Assem-blage	Supersite (informal)
	22	Birds River	Bir 111	Sph 2spp	Tenant Dam
	"	" "	" 211	" "	Cloete Shale
	"	" "	" 311	Hei/Sph	van Biljoen Shale
	23	Bamboesberg	Bam 111	Dic dub	–
	24	Aasvoëlberg	Aas 111	Hei elo	Turner Shale
	"	"	" 211	" "	Proppie Shale
	"	"	" 311	" "	Easter-Egg Shale
	"	"	" 411	Dic/Sph	*Fredlindia* Slate
	"	"	" 511	Dic elo	Erard Slate
	"	"	" 611	Hei elo	Aasvoëlberg Pass
	25	Boesmanshoek Pass	Boe 111	Lep sto	*Equisetum* Ridge
	"	" "	" "	Equ sp	" "
Ka 8	"	" "	" "	Dic/Hei	" "
	"	" "	" 112	Dic cor	*Coriaceum* Flats
	26	Cyphergat	Cyp 111	Dic cra	Open Cast
	"	"	" "	Hei elo	–
	27	Molteno	Mol 111	Sph pon	Slate Quarry
	28	Kleinhoek	Kle 111	Equ sp	Kleinhoek Cutting
	"	"	" "	Hei elo	" "
	"	"	" "	Hei/Dic	" "
	"	"	" 211	Sph pon	Kleinhoek Slate
	29	Kapokkraal	Kap 111	Dic/Ris	–
	30	Kommandantskop	Kom 111	Sph/Dic	–
	31	Kullfontein	Kul 111	Sph pon	–
	32	Telemachus Spruit	Tel 111	Hei elo	–
	33	Vineyard	Vin 111	Dic odo	Homestead
	"	"	" 211	Sch sp	Cheese Factory
	34	Elandspruit	Ela 111	Dic odo	Anne Roadside
	"	"	" 112	Equ sp	Zorba Stream
	"	"	" "	Dic/Hei	" "
	35	Kraai River	Kra 111	Dic odo	Jigsaw Chert
	"	" "	" 211	Equ sp	Plaatkop Track
	"	" "	" 221	beetles	Plaatkop Beetles
	"	" "	" 311	Dic odo	Glenburn
Ka 5	36	Lutherskop	Lut 111	Hei/Dic	Potgieter's Place
	"	"	" 211	Equ sp	Turner's Tributary (1)
	"	"	" 221	" "	" " (2)
	"	"	" 311	Hei elo	Oom-Piet's Campsite
	"	"	" 4111	Equ sp	Orange View
	"	"	" 4112	Hei/Dic	" "
	"	"	" 511	Hei elo	Sonya's Hillock
	37	Nuwejaarspruit	Nuw 111	Equ sp	Clara's Ditch
	"	"	" "	Dic zub	" "
	"	"	" 211	Dic 2spp	Wolfy's Adit
Ka 6	38	Winnaarspruit	Win 111	Hei elo	–
	39	Qualasi Hill	Qua 111	Dic odo	–
	40	Morija	Mor 111	Dic zub	–
	"	"	" "	Dic odo	–
Ka 3	41	Makoaneng	Mak 111	" "	–
	42	Mazenod	Maz 111	Dic cra	Luka
	"	"	" 211	Hei/Dic	Lechesa
Ka 1	43	Golden Gate	Gol 111	Dic dub	–

Tab. 5. Molteno 'localities' and assemblages

Superlocalities: numbered in clockwise order around the Molteno outcrop (see map opposite)
Supersites: arranged chronologically, within each superlocality, according to date of discovery (earliest above)
Assemblages: arranged stratigraphically for each supersite (youngest above)
Informal names: all distinct supersites within a superlocality have been given a familiar name for ease of communication (assemblages within a supersite retain only the formal code name)

Extensiveness of sampling
10 degree squares/subregions (ca 100 km diam. grid)
43 superlocalities (10 km diam. grid)
69 localities (1 km diam. grid)
80 sublocalities (100 m diam. grid)
85 supersites (10 m diam. grid)
100 assemblages (taphocoenoses, TCs)

Tab. 6a,b (see overpage). Molteno gymnosperms, vegetative & reproductive genera (abundance & frequency)

Assemblages (taphocoenoses, TCs): the full set of 100 sampled TCs is arranged in lithostratigraphic order following the 6 recognized sedimentary cycles (& members)
Gymnosperm genera: the 27 foliage genera, 20 ovulate genera & 15 microsporangiate genera are listed in classified sequence
Productive TCs (reproductive genera): 57 of the 100 TCs yield ovulate &/or microsporangiate taxa
Abundance: the relative (% in bold) or absolute (individuals in mild) abundance of genera per TC is recorded within the matrix of the table

Molteno members	Molteno cycles	Tab. 6a. MOLTENO FOLIAGE — assemblage (taphocoenosis)	NON-GYMNOSPERMS: Muscites	Marchantites	Thallites etc.	lycopods	horsetails	ferns	GYMNOSPERMS — Pinopsida: Heidiphyllum	Clariphyllum	Rissikia	Pagiophyllum	Cycadop.: Pseudoctenis	Jeanjacquesia	Ctenis	Moltenia	Ginkgoopsida: Lepidopteris	Scytophyllum	Kurtziana	Dejerseya	Ginkgoites	Paraginkgo	Sphenobaiera	Dicroidium	Kannaskoppifolia	indet.: Batiopteris	Saportaea	Linguifolium	Benn.: Halleyoctenis	Taeniopteris	Gnetopsida: Gontriglossa	Graciliglossa	Cetiglossa	Yabeiella	Jungites	generic diversity: non-gymnosperms	gymnosperms	total
L	6	Ken 111 Dic cra	-	-	-	-	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	99	-	-	-	-	-	-	-	-	-	-	-	2	1	3
TSOMO		Nav 111 Equ sp	-	-	-	-	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
		" " Dic odo	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	98	-	-	-	-	-	-	-	-	-	1	-	-	3	3
		Cal 211 Hei elo	-	-	-	-	-	20	75	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	1	2	3
		" 111 Equ sp	-	-	-	-	99	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	2
	5	" " Dic/Sph	-	-	-	-	-	1	-	-	-	-	-	-	-	-	5	-	-	-	-	-	44	50	-	-	-	-	-	-	-	-	-	-	-	1	3	4
		Bir 211 Sph 2spp	1	-	-	-	-	1	3	-	-	-	-	-	-	-	-	-	-	-	3	-	95	4	-	-	-	2	-	-	-	-	-	-	-	2	5	7
		" 311 Hei/Sph	-	-	-	-	-	-	45	-	-	-	-	-	-	-	-	-	-	-	1	-	40	14	-	-	-	-	1	-	-	-	-	-	-	-	5	5
		" 111 Sph 2spp	40	4	7	4	20	90	10	-	-	-	1	1	-	-	70	-	-	-	43	-	85	1	-	1	-	-	6	70	-	-	-	40	-	11	11	22
		Dor 111 Hei elo	-	-	-	-	-	5	85	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	1	2	3
QIBA	4/5	Gre 121 " "	-	2	-	-	20	2	98	-	-	-	-	-	-	-	-	-	-	2	-	-	-	3	22	-	-	-	-	-	-	-	-	-	-	3	4	7
		" 111 Sph pon	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	5	-	85	-	-	-	-	-	-	-	-	-	-	-	-	-	3	3
		" " Equ sp	1	-	-	-	97	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	2	1	-	-	-	-	-	-	-	-	1	-	4	4	8
		Boe 111 Lep sto	-	-	-	-	-	2	7	-	-	-	-	-	-	-	90	-	-	-	-	-	-	5	-	-	-	3	-	-	-	-	-	5	-	2	5	7
		" " Equ sp	-	-	-	-	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
		" " Dic/Hei	-	-	-	-	-	-	42	-	-	-	7	-	-	-	-	-	-	-	-	-	-	57	-	-	-	-	-	1	-	-	-	1	-	-	5	5
		" 112 Dic cor	-	-	-	-	4	-	14	-	12	-	-	-	-	-	-	-	3	-	-	-	-	99	1	-	-	-	-	-	-	-	-	-	-	1	5	6
		Cyp 111 Dic cra	6	1	-	-	1	4	24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	75	83	20	-	-	-	2	-	-	-	-	-	4	5	9
		" " Hei elo	-	-	-	-	-	-	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
		Mol 111 Sph pon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	99	12	-	-	-	-	-	-	-	-	-	-	-	-	2	2
MAYAPUTI	3	Kan 112 Hei elo	-	-	-	-	6	7	98	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	19	-	-	2	-	1	-	-	-	-	-	4	5	9
		" 111 Ast spA	-	-	-	-	22	63	10	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	2	3	5
		Tel 111 Hei elo	-	1	-	-	48	58	89	-	-	-	-	-	-	-	1	-	-	-	23	-	-	6	33	1	-	-	-	2	-	-	-	-	-	6	7	13
		Kom 111 Sph/Dic	-	1	-	-	15	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	60	39	30	-	-	-	-	-	-	-	-	-	-	3	3	6
		Vin 111 Dic odo	1	-	-	-	-	2	28	-	-	-	3	-	-	-	-	-	7	-	1	-	4	70	2	-	-	-	-	4	-	-	-	-	-	2	8	10
		Ela 111 " "	-	-	-	-	-	4	7	-	-	-	2	-	-	-	5	-	-	-	3	-	1	87	-	-	-	-	-	1	-	-	-	6	-	1	8	9
		Kra 311 " "	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	99	-	-	-	-	-	-	-	-	-	18	-	-	3	3
		" 211 Equ sp	-	-	-	-	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
		" 221 beetles	-	-	-	-	50	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	50	-	-	-	-	-	-	-	-	-	-	-	2	1	3
		" 111 Dic odo	-	-	-	1	-	4	-	-	-	-	-	-	-	-	10	-	4	-	-	-	1	90	-	-	-	-	-	5	-	-	-	-	-	3	5	8
		Lut 111 Hei/Dic	-	-	-	-	10	-	50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	40	-	-	-	-	-	-	-	-	-	-	-	1	2	3
		" 511 Hei elo	-	-	-	-	-	1	80	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	3
		" 4112 Hei/Dic	-	-	-	-	-	-	50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	50	-	-	-	-	-	-	-	-	-	-	-	-	2	2
		" 4111 Equ sp	-	-	-	-	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
		" 311 Hei elo	6	1	-	-	30	3	99	-	-	-	-	-	-	-	19	-	5	-	-	-	29	58	66	-	-	-	-	23	-	-	-	9	-	4	8	12
		" 221 Equ sp	-	-	-	-	99	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	1	2
		" 211 " "	-	-	-	-	80	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	10	-	-	-	4	-	2	3	5
		Tin 121 Sph 2spp	-	-	-	-	1	-	4	-	1	-	-	-	-	-	1	-	-	-	-	-	95	1	-	-	-	-	-	2	-	-	-	1	-	1	7	8
		" 111 Sch sp	-	-	-	-	89	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	3
		" 131 Hei/Ast	-	-	-	-	10	40	50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	3
INDWE (2)	2/3	Wal 111 Dic odo	-	-	-	-	-	-	-	-	-	-	2	1	-	-	2	-	-	-	2	-	3	92	-	-	-	-	-	3	-	-	-	20	-	-	8	8
		Kon 223 " "	-	-	-	-	-	1	1	-	4	-	-	-	-	-	4	-	-	-	4	-	1	80	-	1	-	-	15	-	-	-	-	1	-	5	9	14
		" 222 " "	-	-	2	-	1	1	-	-	9	-	3	-	-	-	9	-	-	-	13	-	10	87	-	-	-	-	8	4	-	-	-	1	-	7	9	16
		" 221 Ast 2spp	-	-	-	1	20	52	-	-	-	-	25	-	2	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	2	-	-	1	-	7	5	12
		" 211 " "	-	-	-	-	20	52	-	-	-	-	21	-	-	-	-	-	-	-	-	-	-	-	4	6	-	10	-	10	3	-	-	-	-	6	6	12
	f	" 211 Hei elo	-	-	-	-	-	-	95	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	2	2
		" 111 Dic odo	-	-	-	1	1	12	7	-	2	-	5	-	-	-	24	-	-	-	-	-	5	78	-	-	-	-	10	1	-	-	-	1	-	3	9	12
		" " Sch sp	-	-	-	-	90	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	2
		" " Hei elo	-	-	-	-	10	-	84	-	-	-	-	-	-	-	-	-	5	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	1	3	4
		Pen 321 Dic/Ris	-	-	-	-	32	5	1	-	35	-	1	-	-	-	9	-	-	-	-	-	5	51	-	-	-	-	5	5	-	-	-	2	-	4	9	13
		" 211 Dic/Equ	-	1	-	-	45	2	2	-	1	-	-	-	-	-	-	-	-	-	-	-	-	50	-	-	-	-	2	-	-	-	-	-	-	4	4	8
		" 221 " "	-	-	-	-	40	20	-	-	2	-	2	-	-	-	-	-	-	-	-	-	-	40	-	-	-	-	-	-	-	-	-	-	-	3	3	6
		" 511 Equ sp	-	-	-	-	98	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	1	1	2
		" 421 Dic odo	-	-	-	-	5	-	4	-	5	-	-	-	-	-	1	-	-	-	-	-	4	89	-	-	-	-	-	2	-	-	-	-	-	1	6	7
		" 431 Dic/Equ	-	-	-	-	40	-	5	-	-	-	5	-	-	-	-	-	-	-	-	-	-	40	-	-	-	-	2	-	-	-	-	-	-	2	4	6
		" 311 Hei elo	6	2	-	-	5	11	75	-	-	-	-	-	-	-	-	-	-	-	-	-	-	25	41	-	-	-	-	-	-	-	-	-	-	5	3	8
		" 411 " "	1	3	-	-	2	3	94	-	-	-	-	-	-	-	-	-	50	-	-	-	-	13	80	-	-	-	-	-	-	-	-	-	-	6	4	10
		Kle 111 Equ sp	-	-	-	-	99	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	2
		" " Hei elo	-	-	-	-	10	-	90	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	2
		" " Hei/Dic	-	-	-	-	-	-	49	-	3	-	-	-	-	-	1	-	-	-	-	-	8	45	-	-	-	-	-	5	-	-	-	-	-	-	6	6
	e	" 211 Sph pon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
		Kul 111 " "	-	-	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	99	-	-	-	-	-	-	1	-	-	-	-	-	2	2	4
		Kap 111 Dic/Ris	-	-	-	-	10	4	25	30	38	-	40	-	-	-	2	-	-	-	-	-	20	50	6	-	-	4	-	3	1	-	-	5	-	3	12	15
		Vin 211 Sch sp	-	-	-	-	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
		Ela 112 Equ sp	-	-	-	-	95	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	2	1	3
	d	" " Dic/Hei	-	-	-	-	10	-	30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	60	-	-	-	-	-	-	-	-	-	-	-	1	2	3
		Nuw 111 Equ sp	-	1	-	-	99	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	2
		" " Dic zub	-	-	-	-	-	4	-	-	2	-	-	-	-	-	-	-	-	-	-	-	30	70	1	-	-	-	-	1	-	-	-	-	-	1	5	6
		" 211 Dic 2spp	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	3	98	-	-	-	-	-	-	-	-	-	-	-	-	4	4
		Win 111 Hei elo	1	-	-	-	2	3	79	-	-	-	-	-	-	-	-	-	-	10	-	-	-	10	4	1	-	-	-	-	-	-	-	-	-	5	5	10
	c	Mor 111 Dic zub	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	99	-	-	-	-	-	1	-	-	-	-	-	1	2	3
		" " Dic odo	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	98	-	-	-	-	-	2	-	-	-	-	-	1	2	3
		Qua 111 " "	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	20	40	-	-	-	-	-	-	-	-	-	5	-	-	4	4
		Mak 111 " "	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-	-	-	-	1	90	-	-	-	-	-	10	-	-	-	-	-	-	4	4
		Maz 111 Dic cra	-	-	-	-	5	3	5	-	-	-	-	-	-	-	2	-	-	-	1	-	12	74	-	-	-	1	-	-	-	-	-	22	-	3	7	10
	b	" 211 Hei/Dic	2	-	-	-	7	4	32	1	-	-	-	-	-	-	1	-	-	-	3	-	1	64	-	-	-	1	-	1	-	-	-	11	-	4	9	13
		Moo 111 Dic zub	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	99	-	-	-	-	-	-	-	-	-	-	-	-	2	2
		Hla 111 Equ sp	-	-	-	-	99	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	1	2
		" 211 Dic 3spp	-	-	-	-	10	1	-	-	1	-	3	-	-	2	1	-	-	-	-	-	7	85	-	-	-	-	-	-	2	-	-	1	-	3	8	11
		" 212 " "	-	-	-	-	1	6	-	-	1	-	1	-	-	4	1	-	-	-	-	-	7	91	-	-	-	1	-	5	1	-	-	-	-	2	9	11
		" 213 Dic elo	3	2	1	3	11	32	1	-	2	-	27	-	-	7	1	-	1	-	-	-	49	89	7	2	-	-	-	6	8	-	-	1	-	16	13	29
		Umk 111 Dic 2 spp	41	26	-	-	2	1	7	20	5	-	1	-	1	41	1	1	18	-	-	-	5	69	42	2	-	-	-	55	5	13	3	45	-	19	18	37
		Cha 111 Dic odo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	-	-	-	-	-	-	-	-	-	-	-	-	1	1
		" 211 Dic dub	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	80	-	-	-	-	-	-	-	-	-	-	-	1	1	2
		Inj 111 Dic odo	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	-	-	-	-	-	4	-	-	-	2	-	1	3	4
		" 211 Dic dub	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	90	-	-	-	-	-	1	-	-	-	-	-	-	3	3
		San 111 Dic cra	1	-	-	-	2	1	5	-	-	-	1	-	-	-	1	-	1	-	5	3	-	90	3	-	-	-	-	2	-	-	-	2	-	3	10	13
		Mng 111 Dic 2spp	-	-	-	-	-	-	6	-	2	-	-	-	-	-	-	-	-	-	2	-	6	93	-	-	-	-	-	2	-	-	-	-	-	-	6	6
		Qac 111 Hei/Dic	1	-	-	-	-	2	50	-	-	-	-	-	-	-	-	-	-	-	-	-	8	50	-	-	-	-	-	-	-	-	-	-	-	2	3	5
		Mat 111 Dic dub	1	-	1	1	20	7	4	-	-	-	12	-	-	-	1	-	3	-	25	-	18	89	2	-	-	-	-	2	-	-	-	2	-	9	10	19
	a	Gol 111 " "	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	99	-	-	-	-	-	1	-	-	-	-	-	-	2	-
		Lit 111 Dic/Hei	14	2	-	-	10	10	23	-	40	-	48	6	-	1	1	-	-	20	4	40	1	50	56	-	1	17	8	78	30	-	-	6	18	6	19	25
BAMBOESBERG	1	Aas 611 Hei elo	-	-	-	-	-	1	80	-	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	3
		" 111 " "	-	17	-	-	10	20	77	-	-	-	-	-	-	-	-	-	-	-	-	-	1	7	2	-	-	-	-	2	-	-	-	-	-	6	5	11
		" 211 " "	10	6	-	-	-	2	99	-	-	-	-	-	-	-	-	-	-	14	-	-	-	-	19	-	-	-	-	-	-	-	-	-	-	3	3	6
		" 311 " "	18	13	-	-	-	2	99	-	1	-	-	-	-	-	-	-	-	-	-	-	1	15	[illegible]	1	-	-	-	-	-	-	-	-	-	4	6	10
		" 411 Dic/Sph	-	5	3	50	75	24	1	-	25	2	13	-	-	-	7	-	15	-	41	-	30	60	150	-	-	-	40	1	-	-	-	75	-	7	13	20
		" 511 Dic elo	-	-	-	-	-	-	20	-	-	-	-	-	-	-	10	-	-	-	-	-	20	50	-	-	-	-	-	-	-	-	-	1	-	-	5	5
		Ask 111 Equ sp	-	-	1	-	50	9	-	-	-	-	-	-	-	-	20	-	-	-	-	-	1	21	-	-	-	-	-	-	-	-	-	-	-	6	3	9
		Bam 111 Dic dub	-	-	-	-	-	-	1	-	1	-	-	-	-	-	1	-	-	-	-	-	-	98	-	-	-	-	-	-	-	-	-	-	-	-	4	4
		Frequency: Total TCs	18	18	6	7	60	56	62	3	21	1	21	3	2	5	30	1	13	5	19	2	43	75	26	10	1	9	10	38	8	1	1	29	1			

Tab. 6a. Molteno gymnosperms, foliage genera (abundance & frequency)

see p. 9 for notes

Sampling

Molteno members	Molteno cycles	Tab. 6b. MOLTENO ♀ & ♂ fruit		Ovulate genera																				Microsporangiate genera														
				Pinopsida					Ginkgoopsida								indet.			Benn.		Gnet.		Pinopsida					Cy.	Ginkgoopsida						Benn.		
		assemblage	(taphocoenosis)	*Dordrechtites*	*Telemachus*	*Rissikistrobus*	*Gypsistrobus*	*Avistrobus*	*Peltaspermum*	*Matatiella*	*Avatia*	*Hamshawvia*	*Umkomasia*	*Fanerotheca*	*Kannaskoppia*	*Cetifructus*	*Alexia*	*Hlatimbia*	*Hystricia*	*Fredlindia*	*Lindtheca*	*Nataligma*	*Fraxinopsis*	*Fredianthus*	*Lutanthus*	*Odyssianthus*	*Rissikianthus*	*Helvetianthus*	*Androstrobus*	*Antevsia*	*Switzianthus*	*Eosteria*	*Stachyopitys*	*Pteruchus*	*Kannaskoppianthus*	*Cycadolepis*	*Weltrichia*	*Leguminanthus*
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		" 211	" "	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
		" 311	" "	40	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	-	-	4	-	-	-
		" 411	Dic/Sph	100	-	20	5	-	88	1	38	14	7	47	-	-	-	-	1	11	16	-	44	2	1	-	15	-	-	-	2	-	67	3	21	3	-	-
		" 511	Dic elo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Ask 111	Equ sp	-	-	-	-	-	-	-	-	-	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15	-	-	-	-
		Bam 111	Dic dub	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Frequency:	Total TCs	17	18	7	1	1	17	4	6	4	22	27	1	1	1	1	1	3	1	1	18	1	3	1	5	1	2	5	4	4	27	22	12	3	2	1
		Abundance:	Total indivs	413	311	85	5	1	257	17	114	24	503	247	50	2	6	2	1	16	16	4	306	2	5	2	79	6	2	32	54	27	539	425	92	14	3	5

Tab. 6b. Molteno gymnosperms, reproductive genera (abundance & frequency)

see p. 9 for notes

2. FREQUENCY & ABUNDANCE

Differentiating frequency & abundance

The measures of *frequency* and *abundance* are crucial in our endeavour to uncover diversity. Our usage of the terms is quite specific within the context of this work.

Frequency. The measure of frequency of a taxon within the Molteno Fm. is the number of taphocoenoses (TCs or assemblages), out of the total 100 sampled, in which it has been found. Through the Gondwana Triassic it is the number of productive degree squares (subregions), out of the total 85 sampled, in which it has been found.

Abundance. The abundance of a taxon is a measure of the absolute or relative number of individuals recorded or collected from an assemblage, formation, region or continent.

In Gondwana Triassic studies, precise abundance data are available only for the Molteno Fm. For other Gondwana continents, where clear counts of collected individuals are rarely given in the literature, the figures recorded below (Tabs 7a,b) and in the hypodigm tables scattered through the systematic section, are the number of illustrated individuals.

Recording abundance

Fruit. As recorded later (Tabs 9a,b–12), reproductive organs are preserved very much less abundantly than foliage.

Absolute abundance (curated individuals): The number of individual specimens of fruit counted in the curated collection.

Relative abundance (counts per man-hour or day): This is a measure of the rate of appearance of taxa within particular TCs. It is recorded as the number of individuals encountered—while cleaving fossiliferous slabs on site or in the lab—within an hour or day (10 hours). While recognising that collectors work at different rates and with varying acuity, these figures are readily attained and highly instructive.

Foliage

Absolute abundance: The tally of curated individuals of a taxon where it accounts for < 1% of the total vegetative fraction of the assemblage (TC).

Relative abundance: The percentage occurrence (estimated at site) of a taxon where it accounts for 1% or more of the vegetative fraction of the TC.

Ovulate genera CLASS ORDER Genus	Individual counts					
		←SAf→				
	SAm	Molt.	other	Ind	Aus	Ant
PINOPSIDA (Coniferopsida)						
DORDRECHTITALES						
Dordrechtites	-	413	-	-	4	-
VOLTZIALES						
*Voltziopsis**	-	-	1	-	6	-
Telemachus	3	311	-	-	4	5
PINALES (Coniferales)						
Rissikistrobus	-	85	-	-	1	-
Gypsistrobus	-	5	-	-	-	-
Avistrobus	-	1	-	-	-	-
*Parasciadopitys**	-	-	-	-	-	2
GINKGOOPSIDA						
PELTASPERMALES						
Peltaspermum	2	257	-	-	3	-
MATATIELLIALES						
Matatiella	-	17	-	-	24	-
GINKGOALES						
*Karkenia**	-	-	-	-	1	-
Avatia	-	114	-	-	-	-
HAWSHAWVIALES						
Hamshawvia	1	24	-	-	2	-
UMKOMASIALES						
Umkomasia	9	503	-	-	61	1
Fanerotheca	13	247	-	-	-	-
PETRIELLALES						
*Petriellaea**	-	-	-	-	-	11
Kannaskoppia	-	50	-	-	-	-
ORDER indet.						
Cetifructus	-	2	-	-	-	-
CLASSES indet.						
ALEXIALES						
Alexia	-	6	-	-	-	-
HLATIMBIALES						
Hlatimbia	-	2	-	-	-	-
ORDER indet.						
Hystricia	-	1	-	-	-	-
BENNETTITOPSIDA						
FREDLINDIALES						
Fredlindia	-	16	-	-	5	-
PENTOXYLALES						
Lindtheca	-	16	-	-	-	-
GNETOPSIDA						
NATALIGMALES						
Nataligma	-	4	-	-	-	-
FRAXINOPSIALES						
Fraxinopsis	40	306	-	-	3	-
Total individuals (approx.)	68	2378	1	-	114	19
Total genera	6	20	1	-	11	4

Microsporangiate genera CLASS ORDER Genus	Individual counts					
		←SAf→				
	SAm	Molt.	other	Ind	Aus	Ant
PINOPSIDA (Coniferopsida)						
VOLTZIALES						
Fredianthus	-	2	-	-	-	-
Lutanthus	-	5	-	-	-	-
Odyssianthus	-	2	-	-	-	-
PINALES (Coniferales)						
Rissikianthus	-	79	-	-	-	-
ORDER indet.						
Helvetianthus	-	6	-	-	-	-
CYCADOPSIDA						
CYCADALES						
Androstrobus	-	2	-	-	-	-
GINKGOOPSIDA						
PELTASPERMALES						
Antevsia	-	32	-	-	-	-
MATATIELLALES						
Switzianthus	-	54	-	-	-	-
GINKGOALES						
Eosteria	-	27	-	-	-	-
HAMSHAWVIALES						
Stachyopitys	4	539	-	-	3	-
UMKOMASIALES						
Pteruchus	5	425	-	1	14	1
PETRIELLALES						
Kannaskoppianthus	-	92	-	-	?1	-
BENNETTITOPSIDA						
FREDLINDIALES						
Cycadolepis	-	14	-	-	-	-
Weltrichia	-	3	-	-	-	-
Leguminanthus	-	5	-	-	-	-
Total individuals	9	1287	-	1	17	1
Total genera	2	15	-	1	3	1

Tabs 7a,b. Gondwana Triassic (GT) gymnosperms, ovulate & microsporangiate genera

Molteno counts: tally of curated individuals
Non-Molteno counts: includes all illustrated individuals in the Gondwana Triassic literature (based on hypodigms published here); clear counts of collected individuals are rarely given in the literature
Generic list: accounts for all GT genera recognised here;
* the 4 ovulate genera *Voltziopsis*, *Parasciadopitys*, *Karkenia* and *Petriellaea*, unknown in the Molteno, are marked by an asterisk

SAm—South America; SAf—Southern Africa; Ind—India; Aus—Australasia; Ant—Antarctica

Abundance in a single TC	Percent-age	Indivs per man-hours cleaving where < 1%: metric heirarchy	range	Indivs per man-days of cleaving
monodominant	70–100%	–	–	–
co-dominant	20–69%	–	–	–
abundant	6–19%	–	–	–
common	3–5%	–	–	–
sparse	1–2%	–	–	–
rare	–	>1 per 1 man-hour	>1 per <5 man-hours	>1 per < ½ man-day
very rare	–	ca 1 " 10 man-hours	1 " 5–49 "	1 " 1–4 man-days
extremely rare	–	ca 1 " 100 "	1 " 50–499 "	1 " 5–49 "
vanishingly rare	–	ca 1 " 1000 "	1 " 500–4999 "	1 " 50–499 "
infinitely rare	–	ca 1 " 10000 "	1 in over 5000 "	1 in over 500 "

Abundance in a single TC	Examples: Genus	TC	% in TC	Rate in man-hours (10 man-hours cleaving = 1 man-day)	Rate in man-days
monodominant	*Heidiphyllum*	in Aas 311 Hei elo	99%		
co-dominant	*Dicroidium*	" Lit 111 Dic/Hei	50%	–	–
abundant	*Halleyoctenis*	" Kon 223 Dic odo	15%	–	–
common	*Sphenobaiera*	" Kon 111 " "	5%	–	–
sparse	*Lepidopteris*	" Lit 111 Dic/Hei	1%	–	–
rare	*Stachyopitys*	" Kon 222 Dic odo	–	36 indivs in 40 man-hours	9 indivs in 1 man-day
very rare	*Fredlindia*	" " " " "	–	3 indivs in 40 "	ca 1 " " 1 " "
extremely rare	*Fredlindia*	" Aas 411 Dic/Sph	–	11 indivs in 512 "	ca 1 " " 5 " days
vanishingly rare	*Hystricia*	" " " " "	–	1 indivs in 512 "	ca 1 " " 51 " "
infinitely rare	–		–	–	–

Tabs. 8a,b. Abundance scale, foliage and fertile organs

Abundance: 10 categories are applied; the top five (>1%) reflecting relative abundance and the lower five (<1%) absolute abundance.

Percentage: This is an estimate made in the field (less often the laboratory) for taxa yielding over 1% of the total assemblage. In those few instances where fertile taxa occur commonly to abundantly on certain bedding plains (e.g. *Dordrechtites* scales), the actual tally of curated individuals is nevertheless given on the various relevant tables.

Examples: Since foliage occurs very much more abundantly than fruit, the former are used to illustrate the upper half of the scale and the latter the lower half. Both categories of organ may, however, fall anywhere within the scheme.

Individuals per man-hours cleaving: as noted, the lower half of the scale applies primarily to fruit, less often foliage. For less thoroughly sampled TCs, all or nearly all individuals are collected, curated and counted. As the *intensity* of sampling any particular TC increases, so the selectivity for better preserved specimens increases. This process for retention is progressive and commences at *ca* 20 individuals (e.g. *Fraxinopsis* at Kap 111). Where higher figures are indicated (e.g. >50), the retention rate is *ca* 50% (e.g. *Pteruchus* at Mat 111) and for very common species (e.g. *Dordrechtites* scales at Aas 411) the retention figure may drop as low as 10%.

	Ovulate genera	TCs	Indivs	Ref. TC
1	*Fanerotheca*	27	247	Bir 111
2	*Umkomasia*	22	503	Mat 111
3	*Telemachus*	18	311	Tel 111
4	*Fraxinopsis*	18	306	Bir 111
5	*Dordrechtites*	17	413	Lut 311
6	*Peltaspermum*	17	257	Bir 111
7	*Rissikistrobus*	7	85	Umk 111
8	*Avatia*	6	114	Bir 111
9	*Hamshawvia*	4	24	Umk 111
10	*Matatielia*	4	17	Mat 111
11	*Fredlindia*	3	16	Aas 411
12	*Kannaskoppia*	1	50	Kan 111
13	*Lindtheca*	1	16	Aas 411
14	*Alexia*	1	6	Umk 111
15	*Gypsistrobus*	1	5	Aas 411
16	*Nataligma*	1	4	Umk 111
17	*Hlatimbia*	1	2	Hla 213
18	*Cetifructus*	1	2	Umk 111
19	*Hystricia*	1	1	Aas 411
20	Avistrobus	1	1	Bir 111
	Totals		2378	

	Microsporangiate genera	TCs	Indivs	Ref. TC
1	*Stachyopitys*	27	539	Bir 111
2	*Pteruchus*	22	425	Umk 111
3	*Kannaskoppianthus*	12	92	Lut 311
4	*Rissikianthus*	5	79	Pen 321
5	*Antevsia*	5	32	Maz 211
6	*Switzianthus*	4	54	Lit 111
7	*Eosteria*	4	27	Aas 311
8	*Cycadolepis*	3	14	Kon 222
9	*Lutanthus*	3	5	Lut 311
10	*Weltrichia*	2	3	Kon 222
11	*Androstrobus*	2	2	Pen 321
12	*Helvetianthus*	1	6	Lit 111
13	*Leguminanthus*	1	5	Kon 222
14	*Odyssianthus*	1	2	Tel 111
15	*Fredianthus*	1	2	Aas 411
	Totals		1287	

Tabs 9a,b. Molteno fertile genera, frequency and abundance

Genera: arranged according to decreasing frequency, then decreasing abundance, then man-hours (see Tab. 11)

Taphocoenoses (TCs): number of TCs in which genus is known

Individuals (indivs): total tally of specimens from all TCs

Reference taphocoenosis (RTC): that TC yielding the best sampled palaeodeme(s) for the genus

Total individuals: ♀ ca 2378; ♂ ca 1287

Relative abundance of the rarest genera

Ovulate genera. The nine least frequent and abundant ovulate genera in the Molteno—each occurring in only one TC—vary considerably in absolute (1–50 individuals) and relative abundance (Tabs 9a, 10). Following our scale of abundance (Tab. 8), *Kannaskoppia* is '*rare*', appearing at a rate of two individuals per man-hour; *Hlatimbia* and *Lindtheca* are '*very rare*'; *Alexia, Nataligma, Gypsistrobus* and *Cetifructus,* each appearing at a rate of one individual within the range 50–499 man-hours, are all '*extremely rare*', while *Hystricia* and *Avistrobus* are the rarest of all recorded Molteno ovulate genera, each with only one fertile head from one TC in over 500 man-hours cleaving.

Statistical projections suggest that many more genera, still rarer than *Hystricia* and *Avistrobus*, are *preserved* in the Molteno, but are yet to be *observed* (Anderson *et al.* 1996). For the most elusive of these, the category of '*infinitely rare*', i.e. one individual in over 5 000 man-hours, is available.

Microsporangiate genera. The four least frequent and abundant microsporangiate genera in the Molteno, *Leguminanthus* (1 per 10 man-hours), *Odyssianthus* (1 per 45 man-hours); *Helvetianthus* (1 per 100 man-hours), and *Fredianthus* (1 per 250 man-hours), range on our abundance scale from '*very rare*' to '*extremely rare*'.

The rarest of all described microsporangiate species in the Molteno is *Lutanthus robustus*, with one individual from Aas 411 (1 per 512 man-hours). As two other species of *Lutanthus* occur at two further TCs, it is not among the least frequent of genera.

Foliage genera. Of the 27 (+ 1 unnamed) gymnospermous foliage genera recognised in the Molteno, fully one quarter (6 plus 1 unnamed) are known from only a single TC. These scarcest foliage elements range in relative abundance from *very rare* through *extremely rare* to *vanishingly rare*, following much the same pattern as the reproductive genera. *Saportaea*, exclusive to Little Switzerland (Lit 111) and with only a single specimen found in 550 man-hours cleaving, is the rarest of all foliage genera in the collection.

Ovulate genus	TC	Indivs	Sampling intensity	Relative abundance	Abundance scale
Kannaskoppia	Kan 111 Ast spA	50	30 man-hours	2 per 1 man-hour	rare
Hlatimbia	Hla 213 Dic elo	2	60 " "	1 per 30 man-hours	very rare
Lindtheca	Aas 411 Dic/Sph	16	512 " "	1 per 40 " "	" "
Alexia	Umk 111 Dic 2spp	6	400 " "	1 per 66 " "	extremely rare
Nataligma	Umk 111 Dic 2spp	4	400 " "	1 per 100 " "	" "
Gypsistrobus	Aas 411 Dic/Sph	5	512 " "	1 per 102 " "	" "
Cetifructus	Umk 111 Dic 2spp	2	400 " "	1 per 200 " "	" "
Hystricia	Aas 411 Dic/Sph	1	512 " "	1 per 512 " "	vanishingly rare
Avistrobus	Bir 111 Sph 2spp	1	550 " "	1 per 550 " "	" "

Microspor. genus	TC	Indivs	Sampling intensity	Relative abundance	Abundance scale
Leguminanthus	Kon 222 Dic odo	5	40 man-hours	1per 10 man-hours	very rare
Odyssianthus	Tel 111 Hei elo	2	90 " "	1 per 45 " "	" "
Helvetianthus	Lit 111 Dic/Hei	6	550 " "	1 per 100 " "	extremely rare
Fredianthus	Aas 411 Dic/Sph	2	512 " "	1 per 250 " "	" "

Foliage genus	TC	Indivs	Sampling intensity	Relative abundance	Abundance scale
Jungites	Lit 111 Dic/Hei	18	550 man-hours	1 per 30 man-hours	very rare
Graciliglossa	Umk 111 Dic 2spp	13	400 " "	1 per 30 " "	" "
unnamed gnetalean	" " " "	7	400 " "	1 per 60 " "	extremely rare
Cetiglossa	" " " "	3	400 " "	1 per 130 " "	" "
Pagiophyllum	Aas 411 Dic/Sph	2	512 " "	1 per 250 " "	" "
Scytophyllum	Umk 111 Dic 2 spp	1	400 " "	1 per 400 " "	" "
Saportaea	Lit 111 Dic/Hei	1	550 " "	1 per 500 " "	vanishingly rare

Tab. 10. Relative abundance of the rarest Molteno genera

Genera listed: only those genera with a frequency of 1 (occurring in a single TC) are included

Ovulate & microsporangiate genera: for frequency and abundance data see Tabs 6b & 9; and for man-hours cleaving Tab. 1.

Foliage genera: for frequency and abundance data see Tab. 6a; and for man-hours cleaving Tab.1. (See Tab. 12 for further details on the unnamed gnetalean.)

assemblages (taphocoenoses)		Sampling: cleaving (man-hours)	Sampling: catalogued slabs	Ovulate genera: *Fanerotheca* 1	*Umkomasia* 2	*Telemachus* 3	*Fraxinopsis* 4	*Dordrechtites* 5	*Peltaspermum* 6	*Rissikistrobus* 7	*Avatia* 8	*Hamshawvia* 9	*Matatiella* 10	*Fredlindia* 11	*Kannaskoppia* 12	*Lindtheca* 13	*Alexia* 14	*Gypsistrobus* 15	*Nataligma* 16	*Hlatimbia* 17	*Cetifructus* 18	*Hystricia* 19	*Avistrobus* 20	genera per TC ♀	Microsporangiate genera: *Stachyopitys* 1	*Pteruchus* 2	*Kannaskoppianth.* 3	*Rissikianthus* 4	*Antevsia* 5	*Switzianthus* 6	*Eosteria* 7	*Cycadolepis* 8	*Lutanthus* 9	*Weltrichia* 10	*Androstrobus* 11	*Helvetianthus* 12	*Leguminanthus* 13	*Odyssianthus* 14	*Fredianthus* 15	genera per TC ♂
Aas 411	Dic/Sph	512	2176	47	7	-	44	100	88	20	38	14	1	11	-	16	-	5	-	-	-	1	-	13	60	3	21	15	-	2	-	3	1	-	-	-	-	-	2	8
Umk 111	Dic 2spp	400	3592	16	197	-	14	10	17	45	-	7	-	-	-	-	6	-	4	-	2	-	-	10	19	138	-	8	7	-	-	-	-	-	-	-	-	-	-	4
Lit 111	Dic/Hei	550	2173	3	51	-	10	50	11	8	-	2	-	-	-	-	-	-	-	-	-	-	-	7	4	36	9	-	4	50	-	-	-	2	-	6	-	-	-	7
Bir 111	Sph 2spp	550	1927	60	-	-	47	50	67	-	66	-	-	2	-	-	-	-	-	-	-	-	1	7	113	-	-	-	-	-	5	1	-	-	-	-	-	-	-	3
Kap 111	Dic spp	65	1310	40	2	5	26	-	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	6	35	11	-	25	-	-	-	-	-	-	-	-	-	-	-	3
Lut 311	Hei elo	50	589	7	-	-	6	50	7	-	3	1	-	-	-	-	-	-	-	-	-	-	-	6	19	-	16	-	-	-	2	-	2	-	-	-	-	-	-	4
Maz 211	Hei/Dic	85	1087	5	46	-	63	40	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	26	27	-	-	18	-	-	-	-	-	-	-	-	-	-	3
Mat 111	Dic dub	65	1082	6	75	12	-	-	4	-	-	-	6	-	-	-	-	-	-	-	-	-	-	5	31	84	3	-	-	1	-	-	-	-	-	-	-	-	-	4
Kon 222	Dic odo	40	449	1	22	-	-	-	24	2	-	-	-	3	-	-	-	-	-	-	-	-	-	5	35	13	-	-	2	-	-	10	-	1	-	-	5	-	-	6
San 111	Dic cra	30	303	5	4	-	10	15	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	7	5	-	-	1	-	-	-	-	-	-	-	-	-	-	3
Bir 311	Hei/Sph	2	133	2	2	-	5	6	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	5	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Hla 213	Dic elo	60	902	5	32	-	-	-	-	5	-	-	-	-	-	-	-	-	-	2	-	-	-	4	2	20	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Ela 111	Dic odo	10	235	1	1	1	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	8	3	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Cyp 111	Dic cra	100	362	1	2	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	44	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Tel 111	Hei elo	90	581	2	-	40	-	-	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	45	1	4	-	-	-	8	-	-	-	-	-	-	2	-	5
Pen 411	" "	70	204	-	-	50	-	1	-	-	-	-	7	-	-	-	-	-	-	-	-	-	-	3	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	1
" 311	" "	35	155	-	3	17	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Kle 111	Hei/Dic	9	288	1	-	-	1	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Bir 211	Sph 2spp	7	184	1	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tin 121	" "	5	33	1	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Wal 111	Dic odo	50	339	24	-	-	12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	21	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Pen 321	Dic/Ris	35	408	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	-	-	30	-	-	-	-	-	-	1	-	-	-	-	3
Kon 111	Dic odo	34	285	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Maz 111	Dic cra	30	462	6	-	-	27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Kan 111	Ast spA	30	365	-	-	-	-	-	-	-	-	-	3	-	50	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gre 111	Equ sp	25	213	3	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-	-	-	-	-	-	-	2	-	-	-	-	-	-	2
Nuw 111	Dic zub	21	138	-	11	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	2	-	15	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Kra 111	Dic odo	20	380	-	14	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	30	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Hla 212	Dic 3spp	11	217	-	4	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Boe 112	Dic cor	6	179	-	8	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	10	-	1	-	-	-	-	-	-	-	-	-	-	-	2
Mol 111	Sph pon	6	95	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kon 111	Hei elo	4	55	-	-	2	-	18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hla 211	Dic 3spp	4	157	3	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Aas 311	Hei elo	140	528	-	-	-	-	40	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	4	-	-	-	12	-	-	-	-	-	-	-	-	2
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Win 111	Hei elo	20	64	-	-	-	-	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1
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Kra 311	Dic odo	13	159	-	-	-	35	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	8	-	-	-	-	-	-	-	-	-	1	-	-	-	-	2
Gol 111	Dic dub	13	108	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Mor 111	Dic odo	12	214	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	30	1	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Gre 121	Hei elo	10	141	-	-	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	1
Kom 111	Sph/Dic	10	168	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	1
Qua 111	Dic odo	8	140	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Boe 111	Dic/Hei	8	98	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 111	Lep sto	8	77	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nuw 211	Dic 2spp	6	119	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Qac 111	Hei/Dic	4	112	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Ela 112	Dic/Hei	4	41	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aas 611	Hei elo	3	47	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lut 411	Hei/Dic	2	60	-	-	12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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Nav 111	Dic odo	2	60	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vin 111	Dic odo	10	166	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Kle 111	Equ sp	4	35	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
	57 TCs	Total TCs		27	22	18	18	17	17	7	6	4	4	3	1	1	1	1	1	1	1	1	1	-	27	22	12	5	5	4	4	3	3	2	2	1	1	1	1	-

Tab. 11. Molteno ovulate & microsporangiate genera, sampling intensity & biodiversity

Taphocoenoses: the 57 TCs are arranged according to diversity of ovulate genera, then to sampling intensity (man-hours cleaving)

Sampling: two measures of sampling intensity for each TC are recorded (see text for explanation)

Genera: arranged in order of decreasing frequency, then decreasing abundance (see Tabs 9a,b)

Matrix: the absolute abundance (individuals) per TC is recorded

Long-tailed frequency & diversity curves: note the long-tailed curves for both generic frequency in the Molteno and generic diversity per TC—which point to many (*preserved*) genera still awaiting discovery

3. AFFILIATED ORGANS

Reassembling the whole plant

A comprehensive strategy towards seeking out affiliations between dispersed organs in a fossil flora is essential to gaining an insight into the true (natural) diversity (*observed*, *preserved* and *existed*) of that flora (Anderson *et al.* 1996). It is inevitable that the reliability of proposed links between organs will vary considerably—from marginal likelihood of affiliation (Grade 1) to certainty of affiliation through organic attachment (Grade 5). The reliability of each foliage, female or male affiliation documented here is indicated according to the following system.

Criteria for affiliations (elaborated after And. & And. 1985, p. 85)

Judgements concerning affiliations are based on an array of observations. Reliability will depend on the following criteria. (The abbreviations used throughout this volume are given in brackets.)

1. Organic attachment (Org. att.)—Organs that are found in direct organic connection constitute the only irrefutable case for conspecific status.

2. Cuticle correspondence (Cut. cor.)—It is reasonably established that the cuticles of different organs of the same species display like characteristics.

3. Morphological correspondence (Mor. cor.)—In certain instances, diagnostic macroscopic features such as ornamentation, blistering and texture are seen in conspecific organs.

4. Kindred reinforcement (Kin. rein.)—Well authenticated organ affiliations for other genera in the family or order offer a secure foundation for proposing linkage.

5. Mutual occurrence, presence or absence (Mut. occ.)—Where different dispersed organs occur in the same assemblage, the possibility exists that they derive from the same parent species. The likelihood will increase with:

- *coupling frequency*—the number of assemblages in which the mutual occurrence is repeated;
- *mutual abundance*—the mutual dominance or rarity of the organs in question;
- *process of elimination*—the preoccupation of organs in other established affiliations;
- *bedding-plane bonds*—the extent to which the organs are confined to particular bedding planes;
- *assemblage paucity*—the lowering of diversity levels;
- *assemblage autochthony*—the degree to which the assemblage represents a single, local plant association.

Reliability grades (after And. & And. 1985, p. 85)

The evidence for linking organs ranges from marginal to certain. At the lower end of the range the evidence will be slim, yet suggestive, or alternate options might be more or less equally likely, while at the upper end of the range clear organic attachment certifies linkage.

Grade 1, *marginal*	– Marginal likelihood of affiliation: mutual occurrence (weak).
Grade 2, *poor*	– Most feasible affiliation (alternatives competitive): mutual occurrence (unclear).
Grade 3, *fair*	– Probable affiliation (alternatives weak): mutual occurrence (fairly clear), little other supportive data.
Grade 4, *good*	– Virtually exclusive likelihood of affiliation: mutual occurrence (particularly clear), cuticle correspondence and/or kindred reinforcement and/or possible organic attachment.
Grade 5, *certain*	– Certain affiliation: organic attachment undoubted.

Organic attachment is known for only five gymnospermous genera (generic pairs) in the Gondwana Triassic, four from the Molteno and one from Australia.

1. Voltziopsis—NSW, L. Triassic (Townrow 1967b, pl. 1e)
2. Kannaskoppia/Kannaskoppifolia—Molteno (this vol.)
3. Kannaskoppianthus/Kannaskoppifolia—Molteno (this vol.)
4. Hamshawvia/Sphenobaiera—Molteno (this vol.)
5. Stachyopitys/Sphenobaiera—Molteno (this vol.)

Umkomasia unirama (Axsmith *et al.* 2000) falls into affiliation Grade 4 as there are two separate shoots, one bearing the fruit and another the leaves.

Organic attachment, Gondwana Triassic

Extreme rarity of (foliage-fruit) organic attachment

Organic attachment is an exceptionally rare phenomenon in the plant fossil record. Only four instances of mutual attachment, involving two whole-plant genera, occur in our Molteno collections that approach 30 000 catalogued slabs from 100 TCs. In the first instance, several specimens from a restricted pocket of silty sediment (at Kan 111 Ast spA) occur, while in the latter three cases (at three different TCs) only single specimens have been found. Just two whole-plant genera are involved.

Kannaskoppia/Kannaskoppifolia/Kannaskoppianthus

Kan 111: *Kannaskoppia/Kannaskoppifolia* (pl. 104)

This taxon provides the finest example, from amongst the wide diversity of gymnospermous plants found in the formation, of specimens that clearly show organic attachment between foliage and female fruit. Several specimens of slender stems from Kan 111 Ast spA bear short shoots with both leaves and female strobili (Grade 5 affiliation).

Kom 111: *Kannaskoppianthus/Kannaskoppifolia* (pl. 108, 109)

One further TC (Kom 111 Sph/Dic) has yielded a single specimen consisting of four *Kannaskoppifolia* leaves and two undoubted strobili of *Kannaskoppianthus* attached to a shoot. An additional 28 specimens of individual leaves of the same species, but different from those from Kan 111, occur in the assemblage.

Hamshawvia/Sphenobaiera/Stachyopitys

Aas 411: *Hamshawvia/Sphenobaiera* (pl. 71)

From Aas 411 Dic/Sph, one specimen shows a cluster of *Sphenobaiera* leaves and a small bifurcate female strobilus attached to the terminal portion of a shoot. The incomplete strobilus is comparable to *Hamshawvia* but clearly smaller and is most likely either an immature or undeveloped specimen of that genus. In view of this uncertainty, we rate the affiliation Grade 4/5 rather than 5.

Maz 111: *Stachyopitys/Sphenobaiera* (pl. 81)

A single specimen from Maz 111 Dic cra shows a *Stachyopitys* strobilus (male) and an incomplete *Sphenobaiera* leaf attached to a bulbous base (Grade 5 affiliation).

There exists supporting evidence from Australia and Eurasia (pp. 213, 218) for the mutual occurrence or attachment of *Sphenobaiera* and its reproductive counterparts.

Relative occurrence of different organs

Paucity of male versus female strobili

It is a conspicuous feature seen in the gymnosperm component of many fossil floras that the male strobili are less diverse, less frequent and less abundant than the female strobili. This is true also of the Molteno flora, but not so markedly as we initially thought. The further our studies of the reproductive structures have progressed, the more prominent has become the male presence. As indicated in the text table below, the females outnumber the males in all respects, but the actual discrepancy varies significantly. As one works down through the taxonomic ranks, from class to genus, the deviation between female and male in *observed* diversity diminishes steadily and markedly (from 2:1 down to 1.3:1). At species level it increases again slightly to 1.5:1. Females outnumber the males in frequency (at a ratio of 1.6:1) and in abundance (2:1). The shape of the frequency curves (distributions) for ovulate and microsporangiate strobili is very similar (Tab. 11) in that both decline rapidly from occurrences in *ca* 25% of TCs to a long tail of rare to single appearances.

We note two further general examples reaffirming this relative paucity of male cones. The first is in the order Voltziales, prominent globally from the U. Permian to M. Jurassic, and the second in the order Glossopteridales, dominant throughout the Gondwana Permian. In the Voltziales only three genera of male strobili to 15 female genera are known (And. & And. 1989, p. 422). In the Glossopteridales the proportion of described male to female genera is one to ten (And. & And. 1985, p. 107).

Paucity of strobili versus foliage

The vegetative component in compression-impression floras such as those preserved in the Molteno far outstrips in all measures the reproductive component. The discrepancy increases rapidly from class (foliage:female = 8:8 = 1:1) through to species (foliage:female = 113:51 = 2.2:1). This will be a reflection partly of straight biomass (frequency and abundance) of the original living material (biocoenosis) and partly due to differential taphonomic filtering (reflected in the taphocoenosis). Foliage palaeodemes outnumber ovulate palaeodemes 3:1 (440:152), while foliage individuals outnumber ovulate individuals (excluding dispersed seeds or scales) at least in the order of 100:1 (250 000:2 378).

Foliage/fruit discrepancy in species diversity

We consider here (following a particular case study) the apparent discrepancy between foliage, female and male species diversity. The pattern for species of Molteno Ginkgoopsida—a clear reversal of that seen in the Pinopsida—is for greater diversity in the foliage than in the female or male fruit. The whole-plant *Peltaspermum/Lepidopteris* presents an exception to this rule: for *Peltaspermum* we define five species, for *Lepidopteris* only two species, and for *Antevsia* one species. The male, *Antevsia*, occurs particularly infrequently and rarely, and the affiliation with *Lepidopteris* is less sure (Grade 3).

What is the reason for this apparent *Peltaspermum-Lepidopteris* diversity anomaly? Is it simply a reflection of imperfect taxonomic decisions reflected in our monograph (And. & And. 1989) on the gymnospermous foliage of the Molteno a decade ago, when our *Peltaspermum* collections were significantly less complete? We witness here that the morphologically simpler *P. monodiscum* occurs far more widely in the Molteno than the more complex *P. tridiscum*, *P. turbanatum* and *P. quindiscum*, which appear to have been restricted to different specific habitats. In referring back to the foliage of the relevant localities (TCs), the question is whether we can now identify further morphological differences suggesting greater species-level diversity. Does the cuticle contribute to resolving the issue? These issues are partly addressed below.

Little Switzerland (Lit 111) & Umkomaas Valley (Umk 111): The excellently preserved cuticle from these two TCs clearly supports the identification of two *Lepidopteris* species, *L. africana* and *L. stormbergensis*. From the patterns of occurrence of foliage and fruit at Lit 111 it is most readily interpreted that *P. monodiscum* might affiliate with *L. africana* and *P. quindiscum* with *L. stormbergensis*, while at Umk 111, *L. thomasii* might affiliate with *L. africana* and *P. quindiscum* with *L. stormbergensis*.

Birds River (Bir 111) & Aasvoëlberg (Aas 411): These two lake-deposit TCs both yield the two *Peltaspermum* species *P. monodiscum* and *P. turbanatum*. The *Lepidopteris* palaeodemes from each are well-represented and diverse and may well include more than one natural species (all are included as *L. stormbergensis* at Bir 111 in And. & And. 1989).

Konings Kroon (Kon 111, Kon 222) & Peninsula (Pen 321): The *Lepidopteris* palaeodemes from Kon 111 (pls 41, 42) and Kon 222 (pl. 43) are extensively illustrated in And. & And. (1989). The latter, yielding the reference palaeodeme (24 individuals) of *P. tridiscum*, includes foliage only of the general *L. africana* range—suggesting that this 'species' affiliates with *P. tridiscum*.

Molteno gymnosperms Prominence	Ranks	foliage	female	male	♀ : ♂ deviation	Whole-plant taxa
Diversity (*observed*)	classes	8	8	4	2 : 1	10
	orders	17	18	11	1,6 : 1	23
	families	24	18	13	1,4 : 1	32
	genera	27	20	15	1,3 : 1	38
	species	113	51	35	1,5 : 1	143
Frequency	palaeodemes	440	152	94	1,6 : 1	-
Abundance	individuals	*ca* 250,000	2378	1288	2 : 1	-

Molteno gymnosperms, diversity, frequency & abundance of the three plant organs

Taxonomic ranks: from class to individual

Whole-plant taxa: for classes, orders & families refer to Tab. 30, pp. 54, 55;
for genera & species refer to Tab. 15, p. 21.

WPG	Ovulate genera	TCs	indivs	affil. grade	Foliage genera	TCs	indivs	Microsporangiate genera	TCs	indivs	affil. grade
1	*Kannaskoppia*	1	50	5	*Kann. (folia)*	25		*Kann. (anthus)*	12	92	5
2	*Hamshawvia*	4	24	4/5	*Sphenobaiera*	43		*Stachyopitys*	27	539	5
3	*Umkomasia*	22	503	4	*Dicroidium*	75		*Pteruchus*	22	425	4
4	*Telemachus*	18	311	4	*Heidiphyllum*	62		*Odyssianthus*	2	2	4
5	*Rissikistrobus*	8	85	4	*Rissikia*	21		*Rissikianthus*	5	79	4
6	*Peltaspermum*	17	257	4	*Lepidopteris*	30		*Antevsia*	5	32	3
7	*Fredlindia*	3	16	3	*Halleyoctenis*	10		*Cycadolepis*	3	14	3
	"	-	-	-	"	-	-	*Weltrichia*	2	3	3
8	*Avatia*	6	114	2	*Ginkgoites*	19	250	*Eosteria*	4	27	3
9	*Fraxinopsis*	18	306	4	*Yabeiella*	29		-	-	-	-
10	*Lindtheca*	1	16	3	*Taeniopteris*	38		-	-	-	-
11	*Nataligma*	1	4	3	*Gontriglossa*	8	100	-	-	-	-
12	*Fanerotheca*	26	247	2	*Dicroidium*	?	?	-	-	-	-
13	*Matatiella*	4	17	2	*Kurtziana*	13	150	-	-	-	-
14	*Hlatimbia*	1	2	2	*Batiopteris*	10	70	-	-	-	-
15	-	-	-	-	*Dejerseya*	5	200	*Switzianthus*	4	54	2
16	-	-	-	-	*Pseudoctenis*	21	250	*Androstrobus*	2	2	2
17	-	-	-	-	*Linguifolium*	9	75	-	-	-	-
18	-	-	-	-	*Moltenia*	5	55	-	-	-	-
19	-	-	-	-	*Clariphyllum*	3	51	-	-	-	-
20	-	-	-	-	*Jeanjacquesia*	3	8	-	-	-	-
21	-	-	-	-	*Paraginkgo*	2	43	-	-	-	-
22	-	-	-	-	*Ctenis*	2	3	-	-	-	-
23	-	-	-	-	*Jungites*	1	18	-	-	-	-
24	-	-	-	-	*Graciliglossa*	1	13	-	-	-	-
25	-	-	-	-	*Cetiglossa*	1	3	-	-	-	-
26	-	-	-	-	*Pagiophyllum*	1	2	-	-	-	-
27	-	-	-	-	*Scytophyllum*	1	1	-	-	-	-
28	-	-	-	-	*Saportaea*	1	1	-	-	-	-
29	*Dordrechtites*	17	413	-	-	-	-	-	-	-	-
30	*Alexia*	1	6	-	-	-	-	-	-	-	-
31	*Gypsistrobus*	1	5	-	-	-	-	-	-	-	-
32	*Cetifructus*	1	2	-	-	-	-	-	-	-	-
33	*Hystricia*	1	1	-	-	-	-	-	-	-	-
34	*Avistrobus*	1	1	-	-	-	-	-	-	-	-
35	-	-	-	-	-	-	-	*Lutanthus*	3	5	-
36	-	-	-	-	-	-	-	*Helvetianthus*	1	6	-
37	-	-	-	-	-	-	-	*Leguminanthus*	1	5	-
38	-	-	-	-	-	-	-	*Fredianthus*	1	2	-
	20 genera				27 genera			15 genera			

Tab. 12. Affiliated organs in the Molteno, statistics

Frequency: number of TCs of 100 sampled in Molteno
Abundance: tally of individuals in curated collection;
generally rounded off where >50 (in case of foliage)
= numerous (far >1000 leaves)
= many (>500 leaves)
Affiliation: reliability grade 1 to 5
Whole-plant genera (WPG): in order of affiliation grade, then frequency (TCs), abundance (indivs), & relative abundance (collecting intensity) of female fruit
Organ-genera: in order of frequency (TCs), then abundance (indivs)
Unnamed gnetalean foliage genus: this genus [see And. & And. 1983, *Ginkgophytopsis* spD from Umk III, pl. 10(6)] remains undescribed in the present work; and, with 7 indivs in a single TC, should fall in this table between WPGs 24 & 25 (see Tab. 10 for further details).

Biodiversity implications

The scarcity of established affiliations (Tab. 12)

- Of the 38 gymnospermous *whole-plant* genera recognised in the Molteno, only eight are known from all three organs—female, foliage and male.
- For a further eight *whole-plant* genera, either female/foliage (6 cases) or foliage/male (2 cases) affiliations are established.
- A total of only 16 of 38 *whole-plant* genera are thus represented by more than one of the three organs (i.e. 16 *multi-organ* genera are known).
- Six female genera, four male genera and 12 foliage genera remain without any hint of their affiliated organs.

From observed to preserved diversity

The implications concerning biodiversity that flow from the rarity of reasonably established affiliations are of particular significance in this study. If less than half of all *observed* Molteno *whole-plant* genera are known from two or three *organ-genera*, and over half are based on only a single organ, a long tail of *whole-plant* genera not represented at all can be projected. Considering the high diversity of *preserved* taxa statistically extrapolated from frequency distributions of *observed* taxa (p. 25), the extent of this tail is, indeed, shown to be long.

DIVISION / CLASS / ORDER / Genus — Ovulate	affiliation grade	Foliage	affiliation grade	Microsporangiate
PINOPHYTA (gymnosperms)				
PINOPSIDA (Coniferopsida)				
DORDRECHTITALES				
Dordrechtites	–	–	–	–
VOLTZIALES				
–	–	–	–	*Fredianthus*
–	–	–	–	*Lutanthus*
Telemachus	4	*Heidiphyllum*	4	*Odyssianthus*
–	–	*Clariphyllum*	–	
PINALES (Coniferales)				
Rissikistrobus	4	*Rissikia*	4	*Rissikianthus*
–	–	*Pagiophyllum*	–	–
ORDERS indet. (2 total)				
Gypsistrobus	–	–	–	–
Avistrobus	–	–	–	–
–	–	–	–	*Helvetianthus*
CYCADOPSIDA				
CYCADALES				
–	–	*Pseudoctenis*	2	*Androstrobus*
–	–	*Jeanjacquesia*	–	–
–	–	*Ctenis*	–	–
–	–	*Moltenia*	–	–
GINKGOOPSIDA				
PELTASPERMALES				
Peltaspermum	4	*Lepidopteris*	3	*Antevsia*
–	–	*Scytophyllum*	–	–
MATATIELLALES				
Matatiella	2	*Kurtziana*	–	–
–	–	*Dejerseya*	3	*Switzianthus*
GINKGOALES				
Avatia	2	*Ginkgoites*	3	*Eosteria*
–	–	*Paraginkgo*	–	–
HAMSHAWVIALES				
Hamshawvia	4/5	*Sphenobaiera*	5	*Stachyopitys*
UMKOMASIALES				
Umkomasia	4	*Dicroidium*	4	*Pteruchus*
Fanerotheca	2	*Dicroidium*		–
PETRIELLALES				
Kannaskoppia	5	*Kannaskoppifolia*	5	*Kannaskoppianthus*
ORDER indet.				
Cetifructus	–	–	–	–
CLASSES indet. (5 total)				
ALEXIALES				
Alexia	–	–	–	–
HLATIMBIALES				
Hlatimbia	2	*Batiopteris*	–	–
ORDERS indet. (3 total)				
Hystricia	–	–	–	–
–	–	*Saportaea*	–	–
–	–	*Linguifolium*	–	–
BENNETTITOPSIDA				
FREDLINDIALES				
Fredlindia	3	*Halleyoctenis*	3	*Cycadolepis*
"	2	"	2	*Weltrichia*
–	–	–	–	*Leguminanthus*
PENTOXYLALES				
Lindtheca	3	*Taeniopteris*	–	–
GNETOPSIDA				
NATALIGMALES				
Nataligma	3	*Gontriglossa*	–	–
ORDERS indet. (2 total)				
–	–	*Graciliglossa*	–	–
–	–	*Cetiglossa*	–	–
FRAXINOPSIALES				
Fraxinopsis	4	*Yabeiella*	–	–
–	–	*Jungites*	–	–
20 genera		27 genera		15 genera

Tab. 13. Affiliated organs in the Molteno, classification

Female/foliage/male affiliates: established in eight cases
Female/foliage affiliates: established in six cases
Foliage/male affiliates: established in two cases

4. MEASURING BIODIVERSITY

Observed diversity (gymnosperms)

'*Because they are subject to different controls, the individual organs (leaves, pollen, fruit etc.) will tend to supply complementary information*' (Ferguson 1992). In considering the *observed* diversity of Molteno gymnosperms, the three organs, foliage, female fruit and male fruit, are individually and collectively accounted for (Tab. 15). It is assumed, for this purpose, that the affiliations reflected in Tab. 13 have been correctly established. Intriguingly, and for unclear taphonomic or morphologic reasons, different organs show greater or lesser levels of *observed* diversity within the different orders or classes. A broad pattern emerges from our work in this regard: the males appear more diverse in the more primitive groups (Pinopsida), the females more diverse in certain of the more advanced groups (e.g. Peltaspermales and Fraxinopsiales), and the foliage more diverse in the Umkomasiales.

Foliage. 8 classes, 17 orders, 24 families, 27 genera, 113 species

The foliage comprises by a very wide margin the most abundant element of the gymnosperm flora, far exceeding female and/or male fruit in preserved biomass. With 113 recognised species, the foliage reflects from two to four times the diversity seen in either the female or male fruit, but as the higher taxonomic ranks are progressively considered the relative diversity of the foliage declines.

Female fruit. 8 classes, 18 orders, 18 families, 20 genera, 51 spp.

From generic through to order level, female fruit diversity in the Molteno outstrips that of the male fruit at a proportion averaging around 3:2. There is, however, a clear increase in diversity disparity seen when shifting up through the higher taxonomic ranks (see text tab., p. 17). From the various classes included as incertae sedis through to the Gnetopsida (Tab.15), the females strongly outnumber the males in *observed* richness. Significantly, the males are represented, in this bracket, only in the Fredlindiales.

Male fruit. 4 classes, 11 orders, 13 families, 15 genera, 35 spp.

In the Molteno it is only in the Pinopsida and Cycadopsida that the males show similar *observed* diversity to the females, (males, 6 gen., 12 spp.; females, 5 gen., 14 spp.). It is interesting to observe that while the male pinopsid cones occur exceedingly rarely in the Molteno (apart from a single prolific palaeodeme of *Rissikianthus* from Pen 321), their diversity matches or exceeds that in their female and foliage counterparts.

Whole-plant. 10 classes, 23 orders, 32 families, 38 gen., 143 spp.

In reflecting *whole-plant* diversity at species level, the highest tally amongst the two or three organs for each *multi-organ* genus is taken. These tallies are considered to indicate the minimum numbers of species (MNSs, Tab. 15) in that while the affiliation between *organ-genera* might have been satisfactorily established, the same cannot necessarily be said for all the included *organ-species*. In the case of some of the larger genera (e.g. *Hamshawvia*/*Sphenobaiera*/*Stachyopitys*), in particular, certain ovulate or microsporangiate species may well occur in the collection without foliage affiliates.

In most, but not all genera, the foliage reflects the greatest diversity. While 19 species of *Dicroidium* are recognised, for instance, only eight of *Umkomasia* and three of *Pteruchus* are readily distinguished. As outlined above, however, the males in some instances and the females in others reveal greater diversity than the foliage.

Building or approaching a real idea of the *observed* plant diversity in the Molteno, or any other formation, necessarily involves the consideration of all plant organs—and necessarily a systematic focus on establishing the patterns of affiliation between these organs.

Unaffiliated seeds

This section on the unaffiliated seeds (Tab. 14, pls 149–151) is included to provide further insight into biodiversity at generic and order level. Seeds that show no evident affiliation with any of the described taxa at these higher ranks most probably represent additional diversity at these levels.

Only a limited proportion of Molteno seeds are considered here, the criteria for inclusion being:

- no evident affiliation with any ovulate organ has been established;
- the seeds show some clearly distinctive features such as shape or ornamentation (many other more or less nondescript forms occur in the collection);
- they derive from the 22 TCs that have proved most prolific with regard to ovulate organs (Tab. 11), i.e. from Aas 411 down through to Wal 111.

The 10 seed types included are infrequent, mostly occurring in only one TC, and generally rare, mostly with five or fewer specimens. Some of the forms may possibly occur in other TCs not yet closely examined for sparse unaffiliated seeds. It is possible that types 9 and 10 are of animal rather than plant origin. No attempt is made here to describe and name the material formally.

The 'species' of seed recorded are all morphologically very distinctive, and also clearly different from any of the seeds affiliated with the described Molteno fruit. Our conclusion, as noted above, is that there remain a significant number of higher-order taxa of female reproductive structures to be discovered. An additional column for seeds could have been added to Tab. 15 opposite and the question of affiliations, classification, whole-plant genera and diversity expanded accordingly.

	assemblages (taphocoenoses)		man-hours cleaving	genera	Unaffiliated seeds									
					1	2	3	4	5	6	7	8	9	10
1	Aas 411	Dic Sph	512	12	-	-	2	40	1	-	-	3	1	-
2	Umk 111	Dic 2spp	400	10	15	-	-	-	4	-	-	-	-	4
3	Lit 111	Dic/Hei	550	7	4	-	-	-	3	1	30	-	-	-
4	Bir 111	Sph 2spp	550	6	-	-	-	6	-	-	-	-	-	-
5	Kap 111	Dic spp	65	6	-	-	-	-	-	-	-	-	-	-
6	Lut 311	Hei elo	50	6	-	-	-	-	-	-	-	-	-	-
7	Maz 211	Hei/Dic	85	5	-	-	-	-	-	-	-	-	-	-
8	Mat 111	Dic/dub	65	5	-	-	-	-	-	-	-	-	-	-
9	Kon 222	Dic odo	40	5	-	-	-	-	-	-	-	-	-	-
10	San 111	Dic cra	30	5	-	-	-	-	-	-	-	-	-	-
11	Bir 311	Hei/Sph	2	5	-	-	-	-	-	-	-	-	-	-
12	Hla 213	Dic elo	60	4	-	-	-	-	-	-	-	-	-	-
13	Ela 111	Dic odo	10	4	-	-	-	-	-	-	-	-	-	-
14	Cyp 111	Dic cra	100	3	-	-	-	-	-	-	-	-	-	-
15	Tel 111	Hei elo	90	3	-	-	-	5	-	-	-	-	-	-
16	Pen 411	" "	70	3	-	-	-	-	-	-	-	-	-	-
17	" 321	Dic/Ris	35	3	-	-	-	-	1	-	-	-	-	-
18	" 311	Hei elo	35	3	-	-	-	-	-	-	-	-	-	-
19	Kle 111	Hei/Dic	9	3	-	-	4	-	-	-	-	-	-	-
20	Bir 211	Sph 2spp	7	3	-	-	-	-	-	-	-	-	-	-
21	Tin 121	" "	5	3	-	-	-	-	-	-	-	-	-	-
22	Wal 111	Dic odo	50	2	-	2	-	-	-	-	-	-	-	-
	Total individuals				19	2	6	51	9	1	30	3	1	4
	Total assemblages (TCs)				2	1	2	3	4	1	1	1	1	1

Tab. 14. Unaffiliated seeds of the Molteno Fm

Taphocoenoses: the 22 TCs listed are those with the greatest diversity of ovulate fruit (see Tab. 17)

Unaffiliated seeds: included are only the 10 most distinctive seeds (from 22 TCs) for which we have been unable to establish any affiliations

Matrix: the number of curated individual seeds

DIVISION / CLASS / ORDER / Genus / **Ovulate**	species	**Foliage**	species	**Microsporangiate**	species	whole-plant (MNSs)
PINOPHYTA (gymnosperms)						
PINOPSIDA (Coniferopsida)						
DORDRECHTITALES						
Dordrechtites	3	–	–	–	–	3
VOLTZIALES						
–	–	–	–	*Fredianthus*	1	1
–	–	–	–	*Lutanthus*	3	3
Telemachus	6	*Heidiphyllum*	1	*Odyssianthus*	1	6
–	–	*Clariphyllum*	1		–	1
PINALES (Coniferales)						
Rissikistrobus	3	*Rissikia*	2	*Rissikianthus*	4	4
–	–	*Pagiophyllum*	1	–	–	1
ORDERS indet. (2 total)						
Gypsistrobus	1	–	–	–	–	1
Avistrobus	1	–	–	–	–	1
–	–	–	–	*Helvetianthus*	1	1
CYCADOPSIDA						
CYCADALES						
–	–	*Pseudoctenis*	9	*Androstrobus*	2	9
–	–	*Jeanjacquesia*	3	–	–	3
–	–	*Ctenis*	2	–	–	2
–	–	*Moltenia*	4	–	–	4
GINKGOOPSIDA						
PELTASPERMALES						
Peltaspermum	5	*Lepidopteris*	2	*Antevsia*	1	5
–	–	*Scytophyllum*	1	–	–	1
MATATIELLALES						
Matatiella	4	*Kurtziana*	16	–	–	16
–	–	*Dejerseya*	1	*Switzianthus*	2	2
GINKGOALES						
Avatia	1	*Ginkgoites*	6	*Eosteria*	2	6
–	–	*Paraginkgo*	1	–	–	1
HAMSHAWVIALES						
Hamshawvia	4	*Sphenobaiera*	9	*Stachyopitys*	6	9
UMKOMASIALES						
Umkomasia	8	*Dicroidium*	19	*Pteruchus*	3	19
Fanerotheca	4	*Dicroidium*	–	–	–	4
PETRIELLALES						
Kannaskoppia	1	*Kannaskoppifolia*	10	*Kannaskoppianthus*	4	10
ORDER indet.						
Cetifructus	1	–	–	–	1	1
CLASSES indet. (5 total)						
ALEXIALES						
Alexia	1	–	–	–	–	1
HLATIMBIALES						
Hlatimbia	1	*Batiopteris*	5	–	–	5
ORDERS indet. (3 total)						
Hystricia	1	–	–	–	–	1
–	–	*Saportaea*	1	–	–	1
–	–	*Linguifolium*	1	–	–	1
BENNETTITOPSIDA						
FREDLINDIALES						
Fredlindia	1	*Halleyoctenis*	3	*Cycadolepis*	1	3
"		"		*Weltrichia*	2	
–	–	–	–	*Leguminanthus*	1	1
PENTOXYLALES						
Lindtheca	1	*Taeniopteris*	8	–	–	8
GNETOPSIDA						
NATALIGMALES						
Nataligma	1	*Gontriglossa*	1	–	–	1
ORDER indet.						
–	–	*Graciliglossa*	1	–	–	1
–	–	*Cetiglossa*	1	–	–	1
FRAXINOPSIALES						
Fraxinopsis	3	*Yabeiella*	2	–	–	3
–	–	*Jungites*	2	–	–	2
20 genera	51	27 genera	113	15 genera	35	143

Tab. 15. Observed diversity of gymnosperms in Molteno Fm.

Female: 8 classes, 18 orders, 18 families, 20 genera, 51 species
Male: 4 classes, 11 orders, 13 families, 15 genera, 35 species
Foliage: 8 classes, 17 orders, 24 families, 27 genera, 113 species
Whole-plant: 10 classes, 23 orders, 32 families, 38 genera, 143 species

MNSs (minimum number of species): diversity recorded for whole-plant species is a minimum (see text opposite)
Families: excluded from this table in interest of simplification (for complete classification including families see pp. 54, 55)
Multi-organ genera: 16 recognized in Molteno (see Tab. 12, p.18)

The species in palaeobotany

The study of diversity and diversity trends at the level of species will become more meaningful in proportion to the level of objectivity attained in palaeobotanical taxonomy. Current levels of objectivity versus subjectivity can hardly be considered adequate. This can be understood by examining the state of taxonomy within the genus *Dicroidium*.

On Dicroidium *taxonomy & diversity*

As the most prominent (successful) genus in the Gondwana Triassic, *Dicroidium* illustrates particularly well the apparently impenetrable problems involved in resolving species-level taxonomy in palaeobotany. Two comprehensive taxonomic revisions of the genus have been attempted over the past two to three decades and these show little agreement in either the taxa recognised or in diversity reflected (Retallack 1977; And. & And. 1983). Few more recent authors have closely followed either taxonomic treatment especially closely.

Reticulate evolution

In And. & And. (1983, 1989) we concluded that *Dicroidium* reflected a highly complex pattern of reticulate evolution rather than the far clearer patterns of phyletic gradualism or punctuated equilibria. Our taxonomy of the genus, in accounting for species, subspecies and formae was an attempt to reflect this complexity. While we still recognise the highly reticulate pattern, in accordance with our palaeodeme approach, we offer here an optional taxonomy by raising all subspecies to the rank of species. In doing so, our *Dicroidium* taxonomy becomes compatible with the approach adopted for the remainder of the gymnosperm systematics in the present volume.

Retallack 1977.................3 gen., 23 spp., 25 var. (39 taxa in total)
And. & And. 1983/89......1 gen., 10 spp., 17 subspp., 15 formae (32 taxa total)
This volume.....................1 gen., 21 spp., 15 formae (32 taxa total)

	Taxonomy as in Retallack 1977		
	genus	species	variety
1	*Dicroidium*	*brownii*	*brownii*
2	"	"	*barrealense*
3	"	*dubium*	*dubium*
4	"	"	*australe*
5	"	"	*tasmaniense*
6	"	*eskense*	–
7	"	*gouldii*	–
8	"	*incisum*	–
9	"	*lancifolium*	*lancifolium*
10	"	"	*lineatum*
11	"	*narrabeenense*	*narrabeenense*
12	"	"	*bursellii*
13	"	*natalense*	–
14	"	*odontopteroides*	*odontopteroides*
15	"	"	*argenteum*
16	"	"	*crassum*
17	"	"	*moltenense*
18	"	"	*obtusifolium*
19	"	"	*remotum*
20	"	*pinnis-distantibus*	–
21	"	*prolungatum*	–
22	"	*radiatum*	–
23	"	*superbum*	–
24	"	*townrovii*	–
25	"	*zuberi*	*zuberi*
26	"	"	*feistmanteli*
27	"	"	*papillatum*
28	"	"	*sahnii*
29	*Johnstonia*	*coriacea*	*coriacea*
30	"	"	*obesa*
31	"	*dutoitii*	–
32	"	*stelzneriana*	*stelzneriana*
33	"	"	*serrata*
34	"	*trilobita*	–
35	*Xylopteris*	*argentina*	–
36	"	*elongata*	*elongata*
37	"	"	*rigida*
38	"	*spinifolia*	–
39	"	*tripinnata*	–

Tab. 16. *Dicroidium* taxonomy as in Retallack 1977
Diversity: 3 genera, 23 species, 25 varieties

	Taxonomy as in And. & And. 1983, 1989				Taxonomy as adapted in this volume
	genus	species	subspecies	forma	
1	*Dicroidium*	*coriaceum*	*dutoitii*	–	*D. dutoitii* Townrow 1967
2	"	"	*coriaceum*	–	*D. coriaceum* (Johnston 1887) Townrow 1957
3	"	*crassinervis*	*crassinervis*	*stelznerianum*	*D. crassinervis* (Geinitz 1876) And. & And. 1983
4	"	"	"	*obtusifolium*	" " "
5	"	"	"	*trilobitum*	" " "
6	"	"	"	*crassinervis*	" " "
7	"	"	"	*sanifolium*	" " "
8	"	*nondichotoma*	–	–	*D. nondichotoma* And. & And. 1989
9	"	*odontopteroides*	*orbiculoides*	–	*D. orbiculoides* (And. & And. 1983) status nov.
10	"	"	*odontopteroides*	*odontopteroides*	*D. odontopteroides* (Morris 1845) Gothan 1912
11	"	"	"	*koningifolium*	" " "
12	"	"	*lineatum*	–	*D. lineatum* (Ten. Woods 1883) And. & And. 1970
13	"	"	*hlatimbifolium*	–	*D. hlatimbifolium* (And. & And. 1983) status nov.
14	"	*dubium*	*tasmaniense*	–	*D. tasmaniense* (Johnston 1887) And. & And. 1970
15	"	"	*switzifolium*	–	*D. switzifolium* (And. & And. 1983) status nov.
16	"	"	*helvetifolium*	–	*D. helvetifolium* (And. & And. 1983) status nov.
17	"	"	*dubium*	–	*D. dubium* (Feitsm. 1878) Gothan 1912
18	"	*narrabeenense**	–	–	*D. narrabeenense* (Walkom 1925) Jac. & Jac. 1950*
19	"	*zuberi*	–	–	*D. zuberi* (Szajnocha 1888) Archang. 1968
20	"	*hughesi**	–	–	*D. hughesi* (Feistm. 1880) Lele 1962*
21	"	*suberbum*	*superbum*	*townrovii*	*D. superbum* (Shirley 1898) Townrow 1957
22	"	"	"	*superbum*	" " "
23	"	"	"	*bipinnatum*	" " "
24	"	"	"	*tripinnatum*	" " "
25	"	"	*mazenodifolium*	–	*D. mazenodifolium* (And. & And. 1983) status nov.
26	"	*elongatum*	*elongatum*	*remotipinnulium*	*D. elongatum* (Carruth. 1872) Archang. 1968
27	"	"	"	*spinifolium*	" " "
28	"	"	"	*rotundipinnulium*	" " "
29	"	"	"	*elongatum*	" " "
30	"	"	*matatifolium*	–	*D. matatifolium* (And. & And. 1983) status nov.
31	"	"	*argentinum*	–	*D. argentinum* (Kurtz 1921) And. & And. 1970
32	"	"	*dimorphum*	–	*D. dimorphum* (And. & And. 1983) status nov.

Tab. 17. *Dicroidium* taxonomy as in And. & And. 1983, 1989 & this volume
Diversity: 10 species, 32 infra-generic taxa total (And. & And. 1983, 1989)
21 species, 32 " " " " (this volume)
* *species not occurring in Molteno Fm.*

On Kannaskoppifolia *taxonomy & diversity*

Kannaskoppifolia is the fifth most prominent gymnosperm foliage genus in the Gondwana Triassic (see section on *Prominence*, pp. 26–29). Of all the Gondwana Triassic genera, it provides the best case study for exploring approaches to infrageneric taxonomy and for probing the problem of recognising *observed* diversity. The genus, newly described in this volume, approaches the ideal for a wide range of reasons:

- *generic integrity*—with its unique foliage (shape and reticulate venation) with cuticle showing transversely oriented stomata, there is little doubt as to the generic integrity of the taxon;
- *organic attachment*—all three organs, foliage, female and male fruit, are known with certainty through organic attachment;
- *morphometrics*—both foliage and male strobili display obvious diversity, with convenient, easily measured morphological features;
- *frequency and abundance*—in that the taxon occurs frequently, yet not too frequently, and fairly commonly, yet not abundantly, the database remains manageable;
- *autecology*—the plant occurs in a spectrum of identified habitats, with different 'species' characterising each.
- *affiliations and conspecificity*—the foliage, in 26 of the 100 Molteno TCs, and male strobilus, in 12 Molteno TCs (invariably co-occurring with the foliage), offer the clear opportunity for analysing conspecificity of organs. (The female strobilus remains known in only one Molteno TC and is not subject to similar analysis.)

We discuss aspects of *Kannaskoppifolia* taxonomy with the purpose of reflecting on the 'species' in palaeobotany. Can we arrive at a reasonably objective and stable concept of the species? Is it possible to find an approach that can be followed by all researchers to arrive at the same result given the same collection of specimens? How closely will this reflect the 'species' in nature?

Kannaskoppifolia *species, habit & habitat*

We recognise 10 species of *Kannaskoppifolia* foliage in the Molteno (And. & And., in prep.). These are recorded in the matrix table (Tab. 18) below, showing TCs, habitat preferences, frequency, abundance, dominant associated genera and man-hours cleaving. The female strobilus, from only a single TC, clearly represents a single species. The male strobilus, with 92 individuals from 12 TCs, is not as diverse morphologically as the foliage and only four species are recognised (pp. 292, 293).

The frequency of the 10 foliage species is very variable—with *K.* sp. E (Pen 311) occurring in 14 of the 26 TCs yielding the genus; and, at the other end of the scale, *K.* sp. C (Umk 111), *K.* sp. G (Umk 111) and *K.* sp. I (Kan 112) each occurring in only a single TC. Based on a spectrum of clues (And. & And., in prep.), we consider the *Kannaskoppia*/*Kannaskoppifolia* plant to be a herbaceous pioneer—from a slender creeper to a free-standing herb—appearing in clearings and newly disturbed sites in a range of habitats. It is associated mostly with *Dicroidium* riparian forest, *Heidiphyllum* thicket and fern/*Kannaskoppifolia* meadows; and very infrequently with *Dicroidium* open woodland, *Sphenobaiera* lakeside woodland and *Equisetum* marsh.

As for the species of most extant genera occupying a particular region or biome, those of *Kannaskoppifolia* in the Molteno might each be anticipated to fill a distinctive niche or ecozone. With extensive and intensive sampling of *Kannaskoppia*/*Kannaskoppifolia* from the Molteno and with systematic interpretation of the relevant sites (assemblages, deposition, and taphonomy) it should be possible to derive a taxonomy that reasonably reflects reality as it existed in the original Molteno floodplain. We submit that an objective methodology towards the recognition of infrageneric taxa—not far removed from practice in extant botany—is attainable.

				species (reference palaeodemes)															Abundance (dominant genera)					
			Kannaskoppifolia	1 *K.* sp A (Pen 311)	2 " sp B (Pen 311)	3 " sp C (Umk 111)	4 " sp D (Cyp 111)	5 " sp E (Pen 311)	6 " sp F (Lit 111)	7 " sp G (Umk 111)	8 " *vinc.* (Kan 111)	9 " sp H (Tel 111)	10 " sp I (Kan 112)	" spp indet	♀ *Kannaskoppia*	♂ *Kannaskoppianthus*	Habitat preference	Frequency (no. of TCs)	*Dicroidium*	*Sphenobaiera*	*Heidiphyllum*	horsetails	ferns	man-hours cleaving
1	Umk 111	Dic 2spp	42	-	-	19	-	21	-	1	1	-	-	-	-	-	*Dicr.* riparian forest (type 1)	2 of 2 TCs	**69**	**5**	**7**	**2**	**1**	400
2	Lit 111	Dic/Hei	56	-	-	-	-	-	55	-	1	-	-	-	-	9			**50**	**1**	**23**	10	10	550
3	Kap 111	Dic/Ris	6	-	-	-	-	6	-	-	-	-	-	-	-	-	*Dicr.* riparian forest (type 2)	4 of 8 TCs	**50**	20	25	**10**	4	65
4	San 111	Dic cra	3	-	-	-	-	2	1	-	-	-	-	-	-	-			**90**	-	**5**	2	1	30
5	Hla 213	Dic elo	7	-	-	-	-	2	4	-	1	-	-	-	-	-			**89**	49	**1**	11	32	60
6	Mat 111	Dic dub	**2**	-	-	-	-	-	17	-	**2**	-	-	-	-	3			**89**	18	**4**	20	7	65
7	Cyp 111	Dic cra	83	-	-	-	80	-	1	-	2	-	-	-	-	-	*Dicr.* open woodland	4 of 35 TCs	**75**	-	**24**	-	4	100
8	Vin 111	Dic odo	2	-	-	-	-	-	-	-	2	-	-	-	-	-			**70**	4	**28**	-	2	10
9	Nuw 111	Dic zub	1	-	-	-	1	-	-	-	-	-	-	-	-	-			**70**	**30**	-	-	4	21
10	Boe 112	Dic cor	1	1	-	-	-	-	-	-	-	-	-	-	-	-			**99**	-	14	4	-	6
11	Aas 411	Dic/Sph	150	-	-	-	-	150	-	-	-	-	-	-	-	21	lake margin	1 of 10 TCs	**60**	**30**	**1**	75	24	512
12	Aas 111	Hei elo	**2**	-	-	-	-	**2**	-	-	-	-	-	-	-	21	*Heidiphyllum* thicket	10 of 24 TCs	7	1	**77**	10	**20**	40
13	" 211	" "	19	-	-	-	-	18	-	-	1	-	-	-	-	1			-	-	**99**	-	2	35
14	" 311	" "	26	-	-	-	-	25	-	-	1	-	-	-	-	4			15	9	**99**	-	2	100
15	Pen 311	" "	41	2	5	-	-	34	-	-	-	-	-	-	-	-			**25**	-	**75**	5	11	35
16	" 411	" "	80	-	10	-	-	70	-	-	-	-	-	-	-	4			13	-	**94**	**2**	**3**	70
17	Kan 112	" "	19	1	2	-	-	10	-	-	-	2	4	-	-	5			**1**	-	**98**	6	7	15
18	Gre 121	" "	22	-	-	-	-	22	-	-	-	-	-	-	-	2			3	-	**98**	20	2	10
19	Win 111	" "	4	-	-	-	1	3	-	-	-	-	-	-	-	-			**10**	-	**79**	2	3	20
20	Tel 111	" "	33	1	2	-	-	-	-	-	-	30	-	-	-	4			**6**	-	**89**	48	58	90
21	Lut 311	" "	66	-	-	-	66	-	-	-	-	-	-	-	-	16			58	29	**99**	30	3	50
22	Gre 111	Equ sp	1	-	-	-	-	-	-	-	-	-	-	1	-	-	*Equis.* marsh	1 of 18 TCs	**2**	-	-	**97**	**1**	25
23	Cal 211	Hei/Ast	**5**	-	-	-	-	-	-	-	**5**	-	-	-	-	-	fern/*Kannask.* meadow	4 of 4 TCs	-	-	**75**	-	**20**	2
24	Kan 111	Ast spA	**5**	-	-	-	-	-	-	-	**5**	-	-	-	50	-			-	-	**10**	**22**	**63**	30
25	Kom 111	Sph/Dic	30	-	-	-	29	-	1	-	-	-	-	-	-	2			**39**	**60**	-	15	**1**	10
26	Kon 211	Ast 2spp	4	-	-	-	-	4	-	-	-	-	-	-	-	-			-	-	-	**20**	**52**	14
Total assemblages			26	4	4	1	5	14	6	1	10	2	1	1	1	12								
Total individuals				6	19	19	177	**3**	79	1	**12**	32	4	1	50	92								

Tab. 18. *Kannaskoppia* in the Molteno, taxonomy, diversity & habitat

Reference taphocoenosis		Whole-plant genus (in systematic sequence)	Diversity in reference taphocoenosis: Foliage gen.	spp	♀ gen.	spp	♂ gen.	spp	insects indivs	spp
Aas 311	Hei elo	*Telemachus/Heidiphyllum*	10	11	1	1	2	2	146	31
Pen 321	Dic/Ris	*Rissikistrobus/Rissikia*	13	18	2	2	3	3	251	12
Maz 211	Hei/Dic	*Peltaspermum/Lepidopteris*	13	19	5	6	3	3	372	34
Pen411	Hei elo	*Matatiella/Kurtziana*	10	11	3	3	1	1	9	5
Wal 111	Dic odo	*Avatia/Ginkgoites*	8	11	2	2	1	2	4	1
Bir 111	Sph 2spp	*Hamshawvia/Sphenobaiera*	22	30	7	9	3	5	474	99
Umk 111	Dic 2spp	*Umkomasia/Dicroidium*	37	75	10	14	4	5	166	42
Kan 111	Ast spA	*Kannaskoppia/Kannaskoppifolia*	5	7	2	2	-	-	-	-
Hla 213	Dic elo	*Hlatimbia/Batiopteris*	29	43	4	7	2	4	52	27
Kon 222	Dic odo	*Fredlindia/Halleyoctenis*	16	22	5	6	6	9	26	10
Aas 411	Dic/Sph	*Lindtheca/Taeniopteris*	20	30	14	16	8	10	129	43
Kon 211	Ast 2spp	*Nataligma/Gontriglossa*	12	11	-	-	-	-	-	-
Kap 111	Dic/Ris	*Fraxinopsis/Yabeiella*	15	19	6	6	3	4	178	43

Tab. 19a. Reference taphocoenoses selected for 13 whole-plant genera, emphasis on classification

Sequence: TCs arranged according to systematic sequence of genera
Whole-plant genera: all 13 established ♀ pairs included
(it should be noted that 16 whole-plant genera are recognized in total if the ♂ pairs are added)
Horizontal divisions: group the genera into taxonomic classes

Reference taphocoenosis		Whole-plant genus (in diversity sequence)	Diversity in reference taphocoenosis: Foliage gen.	spp	♀ gen.	spp	♂ gen.	spp	insects indivs	spp	diversity grade plants)
Umk 111	Dic 2spp	*Umkomasia/Dicroidium*	37	75	10	14	4	5	166	42	v. high
Hla 213	Dic elo	*Hlatimbia/Batiopteris*	29	43	4	7	2	4	52	27	high
Bir 111	Sph 2spp	*Hamshawvia/Sphenobaiera*	22	30	7	9	3	5	474	99	"
Aas 411	Dic/Sph	*Lindtheca/Taeniopteris*	20	30	14	16	8	10	129	43	"
Kon 222	Dic odo	*Fredlindia/Halleyoctenis*	16	22	5	6	6	9	26	10	medium
Kap 111	Dic/Ris	*Fraxinopsis/Yabeiella*	15	19	6	6	3	4	178	43	"
Maz 211	Hei/Dic	*Peltaspermum/Lepidopteris*	13	19	5	6	3	3	372	34	"
Pen 321	Dic/Ris	*Rissikistrobus/Rissikia*	13	18	2	2	3	3	25	12	"
Kon 211	Ast 2spp	*Nataligma/Gontriglossa*	12	11	-	-	-	-	-	-	low
Pen 411	Hei elo	*Matatiella/Kurtziana*	10	11	3	3	1	1	9	5	"
Aas 311	Hei elo	*Telemachus/Heidiphyllum*	10	11	1	1	2	2	146	31	"
Wal 111	Dic odo	*Avatia/Ginkgoites*	8	11	2	2	1	2	4	1	"
Kan 111	Ast spA	*Kannaskoppia/Kannaskoppifolia*	5	7	2	2	-	-	-	-	v. low

Tab. 19b. Reference taphocoenoses selected for 13 whole-plant genera, emphasis on diversity

Sequence: TCs arranged according to total foliage diversity (genera) in reference TCs
Horizontal divisions: group the genera into diversity grades

Diversity grades	
>50 species	v. high diversity
30–49 "	high "
15–29 "	medium "
10–14 "	low "
<10 "	v. low "

Tab. 19c. Diversity grades applied for Molteno TCs

Grades: reflect species diversity (of foliage);
based ideally on optimal sampling

Preserved diversity

What is the gap between the *observed* and the *preserved* diversity in the Molteno Fm.? What is the gap between the number of taxa thus far collected and identified in the Molteno and the total *preserved* diversity assuming a theoretically comprehensive sample of every taxon entombed in the formation?

Fitting the generalised inverse Gaussian-Poisson distribution (GIGP) to the *observed* frequency distribution of taxa, yields estimates of the corresponding *preserved* biodiversity (And. & And. 1995; Anderson *et al.* 1996). Three extrapolations for plants and insects, following this statistical technique, yielded provocative figures:

vegetative species (full flora)—206 *observed*, 667 *preserved*;
ovulate orders (gymnosperms)—16 *observed*, 84 *preserved*;
insects (full fauna)—335 *observed*, 7 740 *preserved*.

The diversity of vegetative species *preserved* in the Molteno appears to be over three times the *observed* tally. The projected leaps from *observed* to *preserved* ovulate-gymnosperm orders and of insect species—five times and 20 times respectively—are even more extreme. Although the Molteno has been unusually well sampled, these data suggest that the uncollected taxa, at all ranks (to order), far outnumber the collected taxa.

Consider the jump from 206 *observed* to 667 *preserved* vegetative species in the Molteno as projected in Anderson *et al.* (1996). Roughly half of these species are gymnosperm and half non-gymnosperm. The projection from *observed* to *preserved* species is roughly three- to four-fold. The projection for *whole-plant* genera may (?)fairly be assumed to follow a similar proportional increase. The tally rises, then, from 38 whole-plant genera *observed* to roughly 125 *preserved* (and to *ca* 250 *existed*).

Though we have sampled 100 TCs, only the tip of the diversity iceberg appears to have been skimmed. This is a crucial observation for a variety of reasons. Consider the origin of angiosperms, for instance. If the earliest stem angiosperms emerged in the Late Triassic and if they remained a very insignificant element of the flora, it is more than likely that current levels of sampling would virtually miss them altogether. The crown angiosperms (non-eudicots including monocots, plus eudicots) in the light of recent molecular-based cladistics (The Angiosperm Phylogeny Group 1998; Nandi *et al.* 1998; Soltis *et al.* 2000; Savolainen *et al.* 2000), are generally accepted as being monophyletic. This reveals nothing, however, of the stem angiosperms and the nature of their tree through the Mesozoic. They may well have been quite diverse with several (perhaps many) major lineages to order level. The initial stages of their evolution will most likely remain largely unobserved within the explosive Late Triassic radiation for many years to come. How many stem-angiosperm lineages (Anderson 1999, p. 53) arose in the Late Triassic that never made it through the Late Triassic extinction events?

Existed diversity (& the taphonomic factor)

Extrapolations suggest that as many as 667 vegetative species, 84 gymnosperm orders and 7 740 species of insects are *preserved* in the Molteno Fm. What diversity of plants and insects actually colonised the intracontinental Molteno braidplain? How many plant and insect taxa that existed in the region during Molteno times were never preserved in the sediments of the formation? What was the measure of the taphonomic filter? We simply do not know. What we can be certain of is that only part of the biocoenosis (original community) is ever represented in the thanatocoenosis (fossil assemblage) (Ferguson 1992).

In And. & And. (1995) we followed a possibly conservative estimate that around half of all taxa living in the Molteno Floodplain Biome were never preserved. In round terms the original Molteno diversity might read:

vegetative species (full flora)—2 000 *existed*
insects (full fauna)—20 000 *existed*

In our 1995 paper we compared the projected Molteno diversity with that recorded in the seven biomes—Desert, Succulent Karoo, Nama-Karoo, Savanna, Grassland, Forest, Fynbos—recognised in extant southern Africa (Gibbs Russell 1987; Rutherford & Westfall 1994). The number of species occurring in the core areas of these biomes varies widely from 497 to 7 316. The Molteno flora, assuming 2 000 species (*existed*), was seen to be on a par with the Succulent Karoo (2 125 species) and the Nama-Karoo (2 147 species) biomes of today.

Though the Molteno Biome was topographically, edaphically and climatically simple and therefore included few vegetation types (ecozones), it apparently supported a diversity at least akin to similar biomes in the extant world.

5. PROMINENCE (colonisation success)

Colonising the Gondwana Triassic (GT)

Wilson (1992, p. 121), in *The Diversity of Life*, handled the concept of success thus: '*Success in biology is an evolutionary idea. It is best defined as the longevity of a species with all its descendants. The longevity of the Hawaiian honeycreepers will eventually be measured from the time the ancestral finch-like species split off from other species, through its dispersal to Hawaii, and finally to that time when the last honeycreeper species ceases to exist.*' This seems altogether too narrow a usage for such an all-embracing term. The success of an individual or institution or civilisation is not measured in terms of its longevity alone. Duration can be only one of several attributes.

The terms *prominence* and *success* are applied in our work synonymously. The *prominence* of a genus in the *Gondwana Triassic Empire* refers to its relative importance or consequence and is measured as the sum of the five attributes—Frequency, Ubiquity, Diversity, Abundance and Longevity (FUDAL).

The DUFA concept was introduced in And. & And. (1989) and is here slightly expanded and shuffled to read FUDAL: an acronym which is fortuitously appropriate ('feudal' essentially referring to the holding of land or, alternatively, to the continuous quarrel or contention between clans).

Vegetative organs

Considering the far wider occurrence of vegetative versus reproductive parts and the uncertainties concerning the affiliation of organs, the FUDAL rating system is based exclusively on the former. While the measure of prominence based on foliage fossils alone may be imperfect, the formula provides a good approximation of the success of the original whole-plant genus.

Attributes of success (Gondwana Triassic)

Frequency (F): measure of repetitiveness of occurrence.
The number of subregions (degree squares), of the 85 across Gondwana yielding Triassic megaplants, from which the genus has been recorded. The tally is derived directly from the distribution maps published here, most being reproduced unchanged from our previous Molteno volumes (And. & And. 1983, 1989).

Ubiquity (U): measure of general range of occurrence.
The number of superregions (continents), of the five making up Gondwana, from which the genus has been recorded.

Diversity (D): measure of speciation, radiation, variability.
The number of species recognised in the genus for the Gondwana Triassic (as documented in this volume).

Abundance (A): measure of quantity.
The norm of the abundance figures for the genus in those assemblages (only those judged to represent largely the local flora) in which it occurs. The data are based exclusively on Molteno assemblages since clear abundance figures are rarely available for other formations.

Longevity (L): measure of duration of the lineage.
The duration in number of international standard ammonite biozones between first and last recorded appearances—as plotted on the stratigraphic figures in this volume. Longevity will probably prove more effectively measured in millions of years, but this is not attempted here as our GT stratigraphic base for plotting generic occurrence still shows only the ammonite biozones (see pp. 7, 45).

Weighting of attributes

As applied here, the five criteria of success are not given equal weight in the FUDAL formula. This is not through design but is simply a consequence of there being 85 productive degree squares across Gondwana, only five extant continents comprising the supercontinent, and *ca* 45–50 million years spanning the Triassic.

Should the criteria be given equal weight and, if so, how? In measuring evolutionary success, should abundance rate higher than frequency or longevity higher than ubiquity, as turns out to be partly or wholly the case in our study? The abundance figures, where only 10 of 27 foliage genera rate 1% or higher, might well gain greater meaning through adjustment.

No attempt is made in this study to introduce adjustments to the numbers. The ratings, as recorded, serve sufficiently our present purpose.

Unequal or under-sampling (& the taphonomic effect)

Lepidopteris, as currently known, occurs very evenly scattered across Gondwana, yet is recorded from only 19 of 84 degree squares, while *Dicroidium* is recorded from 45 degree squares. This discrepancy is almost certainly a reflection of under-sampling or under-reporting. Being far less common than *Dicroidium*, comprising around 1% compared to 90% of assemblages as a norm, more intensive sampling is needed before finding specimens of the genus. *Lepidopteris* is in reality quite probably preserved in as many degree squares as is *Dicroidium*. Similar under-scoring would hold also for other foliage genera.

FUDAL fingerprints

The FUDAL fingerprint (formula) for each genus is clearly distinctive and, along with 'geostrat' occurrence, it tells a great deal about the kind of parent plant being considered. *Dejerseya* (6/2/1/11/2) and *Kannaskoppifolia* (23/3/10/-/26), for instance, could hardly be more different in terms of colonisation, diversification and autecology. *Dejerseya*, interpreted as a shrub to small tree that appeared (apparently) only late in the Triassic, is very infrequent yet common where it occurs and, though morphologically variable, never appears to have had the time to diversify. *Kannaskoppifolia*, seen as a herbaceous pioneer, appeared early in the Triassic and colonised widely through Gondwana during the rest of the period, becoming frequent (though always rare) and well diversified.

Frequency most closely reflects prominence

Of the five attributes defining prominence, frequency (F) is the measure that most closely reflects it. In Tab. 20a, where the 26 Molteno gymnosperm genera are ordered according to decreasing prominence, it is readily seen that they also fall very nearly in correct sequence following decreasing frequency. The prominence hierarchy reflects very closely the frequency hierarchy. In view of this, a first approximation of generic prominence in the Gondwana Triassic can be derived directly from the frequency values. Or put another way, frequency might be considered the primary attribute of prominence or success (at least for the GT) rather than longevity as proposed by Wilson (1992).

Diversity least closely reflects prominence

In contrast to frequency (F), diversity (D) reflects prominence—at least for Gondwana Triassic gymnosperms—least closely. The diversity value for several genera falls far out of sequence when the genera are plotted according to prominence. *Heidiphyllum*, with only three species on the one hand, and *Kurtziana* and *Kannaskoppifolia* with as many as 20 and 10 species, respectively, on the other, fall well out of sequence.

Hier-archy	Molteno foliage genera (gymnosperms)	of 84 F	of 5 U	spp. D	% A	m.yrs. L	Prom-inence	grade
1	*Dicroidium*	45	5	21	90%	27	188	5
2	*Heidiphyllum*	26	5	3	95%	18	147	4
3	*Sphenobaiera*	26	3	12	30%	26	99	
4	*Taeniopteris*	32	5	10	2%	20	69	
5	*Kannaskoppifolia*	23	3	10	-	26	62	
6	*Linguifolium*	18	4	5	-	27	56	
7	*Ginkgoites*	21	4	9	-	17	51	
8	*Lepidopteris*	19	4	5	1%	21	50	3
9	*Pseudoctenis*	16	3	11	3%	14	47	
10	*Yabeiella*	21	3	2	-	17	43	
11	*Rissikia*	17	5	2	1%	14	39	
12	*Kurtziana*	6	2	20	-	2	30	
13	*Gontriglossa*	10	4	1	1%	9	25	
14	*Halleyoctenis*	7	2	4	2%	9	24	
15	*Dejerseya*	7	2	1	11%	2	23	
16	*Paraginkgo*	5	2	1	-	14	22	2
17	*Jungites*	3	2	3	-	13	21	
18	*Batiopteris*	7	3	7	-	2	19	
19	*Saportaea*	3	3	2	-	9	17	
20	*Moltenia*	4	3	4	-	4	15	
21	*Pagiophyllum*	2	2	2	-	6	12	
22	*Ctenis*	4	3	2	-	2	11	
23	*Jeanjacquesia*	3	1	3	-	2	9	
24	*Clariphyllum*	3	1	1	-	1	6	1
25	*Graciliglossa*	1	1	1	-	1	4	
26	*Cetiglossa*	1	1	1	-	1	4	
27	*Scytophyllum*	1	1	1	-	1	4	

Hier-archy	Molteno foliage genera (gymnosperms)	of 84 F	of 5 U	spp. D	% A	m.yrs L	Prom-inence
2	*Heidiphyllum*	26	5	3	95%	18	147
24	*Clariphyllum*	3	1	1	-	1	6
11	*Rissikia*	17	5	2	1%	14	39
21	*Pagiophyllum*	2	2	2	-	6	12
9	*Pseudoctenis*	16	3	11	3%	14	47
23	*Jeanjacquesia*	3	1	3	-	2	9
22	*Ctenis*	4	3	2	-	2	11
20	*Moltenia*	4	3	4	-	4	15
8	*Lepidopteris*	19	4	5	1%	21	50
27	*Scytophyllum*	1	1	1	-	1	4
12	*Kurtziana*	6	2	20	-	2	30
13	*Dejerseya*	7	2	1	11%	2	23
7	*Ginkgoites*	21	4	9	-	17	51
16	*Paraginkgo*	5	2	1	-	14	22
3	*Sphenobaiera*	26	5	12	30%	26	99
1	*Dicroidium*	45	5	21	90%	27	188
5	*Kannaskoppifolia*	23	3	10	-	26	62
18	*Batiopteris*	7	3	7	-	2	19
19	*Saportaea*	3	3	2	-	9	17
6	*Linguifolium*	18	4	5	-	27	56
14	*Halleyoctenis*	7	2	4	2%	9	24
4	*Taeniopteris*	32	5	10	2%	20	69
13	*Gontriglossa*	10	4	1	1%	9	25
25	*Graciliglossa*	1	1	1	-	1	4
26	*Cetiglossa*	1	1	1	-	1	4
10	*Yabeiella*	21	3	2	-	17	43
17	*Jungites*	3	2	3	-	13	21

Tab. 20a,b. Prominence, Molteno foliage genera in Gondwana context

Arrangement: genera in order of decreasing prominence
FUDAL fingerprints: emphasizing the diversity of pattern
Prominence score: ranges vary widely from 188 down to 4
Prominence grade: for discussion of genera in each grade see text

Arrangement: genera in classified order
Horizontal divisions: genera grouped into taxonomic classes

Prominence hierarchy & FUDAL grades

Molteno foliage genera: Only the gymnosperm foliage genera recorded from the Molteno are accounted for here. Only four additional genera, mostly localised and rare, are known from elsewhere in the Gondwana Triassic (And. & And. 1989):

Voltziopsis	Pinopsida	eastern Australia	L. Trias
Pachydermophyllum	Ginkgoopsida	E. Aus, NZ	L-U.Trias
Ptilophyllum	Bennettitopsida	eastern Australia	M. Trias
Zamites	"	" "	" "

Prominence hierarchy: In Tab. 20a, we list the 27 known Molteno gymnosperm foliage genera according to prominence hierarchy. *Dicroidium* and *Heidiphyllum* clearly head the list with prominence figures of 188 and 147 respectively, while *Graciliglossa, Cetiglossa* and *Scytophyllum* occupy the tail, with figures of only 4. *Dicroidium* approaches the theoretical maximum for the Gondwana Triassic Empire, while the latter genera manifest the theoretical minimum.

FUDAL grades: As for abundance and diversity (discussed elsewhere), we apply five grades in categorising the success or prominence of a genus. These are defined as follows:

Grade	Prominence (success grade)	FUDAL score
5	maximum success	>150
4	high success	75–150
3	intermediate success	30–74
2	limited success	15–29
1	minimum success	4–14

On the Molteno genera & their prominence grades

Grade 5: *Dicroidium* stands head and shoulders above all other Gondwana Triassic genera in prominence. As currently known, it is twice as frequent and twice as diverse (aside from *Kurtziana*) as its closest competitors. *Dicroidium* is the overwhelmingly dominant genus in three (riverine forest types 1 and 2, floodplain woodland) of the seven primary habitat types recognised in the Molteno Biome.

Grade 4: *Heidiphyllum* and *Sphenobaiera*, the two genera falling in this category, are the only other gymnospermous taxa dominating particular habitat types in the Molteno.

Grade 3: The nine Molteno genera (*Kurtziana* again being an exception) falling in this category all occur frequently and ubiquitously across Gondwana and spanned nearly half or more of the Triassic. They ranged in diversity from two to 20 species, but were mostly rare, only occasionally reaching 1–3% in abundance.

Grade 2: The eight Molteno genera falling here are distinctly less frequent and ubiquitous than in the previous category. Most are known from only two regions in Gondwana. Other than *Batiopteris*, none apparently diversified with much success. In the four least prominent of these genera, however, each of the few available palaeodemes represents a clearly different species. Abundance is mostly below 1% and longevity spans less than a third of the Triassic.

Grade 1: The seven genera of this category, from *Pagiophyllum* to *Scytophyllum*, are extremely minor components of the Molteno flora and beyond. The last three are each known from only a single assemblage (the Umkomaas Waterfall locality, Umk III).

MOLTENO GYMNOSPERM GENERA			SAm			SAf Molteno			Ind			Ant			Aus		
Female	Foliage	Male	♀	0	♂	♀	0	♂	♀	0	♂	♀	0	♂	♀	0	♂
PINOPSIDA																	
Dordrechtites	—	—	✓	-	-	3	-	-	-	-	-	-	-	-	✓	-	-
—	—	*Fredianthus*	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
—	—	*Lutanthus*	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-
Telemachus	*Heidiphyllum*	*Odyssianthus*	1	2	-	6	1	1	-	1	-	1	1	-	1	2	-
—	*Clariphyllum*	—	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Rissikistrobus	*Rissikia*	*Rissikianthus*	-	1	-	3	2	4	-	-	-	-	1	-	2	2	-
—	*Pagiophyllum*	—	-	-	-	-	1	-	-	1	-	-	1	-	-	-	-
Gypsistrobus	—	—	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Avistrobus	—	—	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
—	—	*Helvetianthus*	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
CYCADOPSIDA																	
—	*Pseudoctenis*	*Androstrobus*	-	3	-	-	9	-	-	1	-	-	-	-	-	6	-
—	*Jeanjacquesia*	—	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-
—	*Ctenis*	—	-	1	-	-	2	-	-	-	-	-	-	-	-	1	-
—	*Moltenia*	—	-	1	-	-	4	-	-	-	-	-	-	-	-	1	-
GINKGOOPSIDA																	
Peltaspermum	*Lepidopteris*	*Antevsia* ✓	-	1	-	5	2	1	-	1	-	-	-	-	1	4	-
—	*Scytophyllum*	—	-	✓	-	-	1	-	-	-	-	-	-	-	-	-	-
Matatiella	*Kurtziana*	—	-	✓	-	4	16	-	-	-	-	-	-	-	✓	✓	-
—	*Dejerseya*	*Switzianthus*	-	-	-	-	1	2	-	-	-	-	-	-	-	1	1
Avatia	*Ginkgoites*	*Eosteria*	-	✓	-	1	6	2	-	1	-	-	-	-	-	4	-
—	*Paraginkgo*	—	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-
Hamshawvia	*Sphenobaiera*	*Stachyopitys*	-	5	✓	4	9	6	-	1	-	-	3	-	1	5	✓
Umkomasia	*Dicroidium*	*Pteruchus*	✓	✓	✓	8	19	3	-	✓	-	✓	✓	✓	✓	✓	✓
Fanerotheca	"	—	✓	-	-	4	-	-	-	-	-	-	-	-	✓	-	-
Kannaskoppia	*Kannaskoppifolia*	*Kannaskoppianthus*	-	✓	-	1	10	4	-	-	-	-	-	-	-	✓	-
Cetifructus	—	—	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
CLASSES INDET.																	
Alexia	—	—	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Hlatimbia	*Batiopteris*	—	-	✓	-	1	5	-	-	-	-	-	-	-	-	✓	-
ORDERS INDET.																	
Hystricia	—	—	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
—	*Saportaea*	—	-	1	-	-	1	-	-	1	-	-	-	-	-	-	-
—	*Linguifolium*	—	-	3	-	-	1	-	-	-	-	-	-	-	-	4	-
BENNETTITOPSIDA																	
Fredlindia	*Halleyoctenis*	*Cycadolepis*	-	-	-	1	3	1	-	-	-	-	-	-	1	1	-
"	"	*Weltrichia*	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
—	—	*Leguminanthus*	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Lindtheca	*Taeniopteris*	—	-	4	-	1	8	-	-	1	-	-	1	-	-	7	-
GNETOPSIDA																	
Nataligma	*Gontriglossa*	—	-	1	-	1	1	-	-	1	-	-	-	-	-	1	-
—	*Graciliglossa*	—	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
—	*Cetiglossa*	—	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Fraxinopsis	*Yabeiella*	—	3	2	-	4	3	-	-	-	-	-	-	-	2	1	-
—	*Jungites*	—	-	1	-	-	2	-	-	-	-	-	-	-	-	-	-

Tab. 21. Molteno gymnosperm genera in Gondwana context, diversity

Molteno genera: arranged to show affiliations
Matrix of table: species diversity as observed in Gondwana Triassic
✓ = presence (diversity unknown)

Colonising the Molteno floodplain

A cursory glance at the table below (Tab. 22) provides a clear indication that only two genera of gymnosperm, *Dicroidium* and *Heidiphyllum* (apart from the horsetails, particularly the single genus *Equisetum*), dominate the Molteno flora. *Sphenobaiera* is a clear, yet distant, third in dominance. It is these four genera—three gymnosperm and one non-gymnosperm—that dominate the major habitats/ecozones recognised in the Molteno Floodplain Biome.

Prominence hierarchy & FAD grades (Tab. 22)

Prominence: Where generic prominence for the *Gondwana Triassic Empire* is scored according to the FUDAL formula, it is scored for the more restricted Molteno Formation according to the FAD (**F**requency + **A**bundance + **D**iversity) formula. The attributes **U**biquity and **L**ongevity do not apply in the narrower geographic space and more limited time frame. It has been shown that frequency most closely reflects prominence for the Gondwana Triassic (Tab. 20a,b) and it is seen to reflect prominence even more closely for the Molteno (Tab. 22). When the 27 Molteno gymnosperm genera are listed in order of decreasing frequency, their FAD-scores hierarchy parallels the sequence almost exactly.

FAD grades: As for the FUDAL system in the case of the Gondwana Triassic, we apply a scheme of 5 FAD grades in categorising the success or prominence of a genus in the Molteno Fm.

Grade	Prominence (success grade)	FAD score
5	maximum success	>100
4	high success	50–99
3	medium success	20–49
2	low success	3–19
1	minimum success	2

Prominence grades (FAD scores)

Comparison of prominence, Molteno & Gondwana Triassic

The prominence hierarchy of the 27 Molteno gymnosperm foliage genera as plotted for the Molteno Fm. in particular, or the Gondwana Triassic in general, is similar, but not identical. The widest discrepancy in the positions of particular genera between the two hierarchies occurs where a taxon has a distinct *centre(s) of prominence* somewhere in Gondwana. Examples include *Saportaea*, ranked 19th in Gondwana and only 26th in the Molteno, with a clear centre of prominence in Argentina; and *Linguifolium*, ranked 6th in Gondwana and only 14th in the Molteno, with centres of prominence in Chile, New Zealand and Queensland along the southern coastal margin of Gondwana.

	Gymnosperm genera	frequency	abundance	diversity	plant form	preferred habitat	Molteno Prominence FAD	Grade
1	*Dicroidium*	75	**90%**	19	shrub to large tree	forest to woodland	184	5
2	*Heidiphyllum*	62	**95%**	1	woody, reed-like	floodplain thicket	158	
3	*Sphenobaiera*	43	**30%**	9	shrub to med. tree	lake margin	82	4
4	*Taeniopteris*	38	**2%**	8	shrub to small tree	forest to woodland	48	
5	*Lepidopteris*	30	**1%**	2	medium shrub	riverine forest	33	
6	*Yabeiella*	29	750	3	large tree	" "	32	
7	*Kannaskoppifolia*	26	750	10	herbaceous pioneer	wide spectrum	36	
8	*Pseudoctenis*	21	**3%**	9	cycad-like (small)	forest to woodland	33	3
9	*Rissikia*	21	**1%**	2	large tree	riverine & wetland	24	
10	*Ginkgoites*	19	250	6	shrub to tall tree	floodplain woodland	25	
11	*Kurtziana*	13	150	16	small tree	" "	29	
12	*Halleyoctenis*	10	**2%**	3	cycad-like	open woodland	15	
13	*Batiopteris*	10	70	5	creeper	wide spectrum	15	
14	*Linguifolium*	9	75	1	herbaceous pioneer	water margin	10	
15	*Gontriglossa*	8	**1%**	1	" "	" "	10	
16	*Dejerseya*	5	**11%**	1	shrub or small tree	forest to woodland	17	
17	*Moltenia*	5	55	4	cycad-like (small)	riverine forest	9	2
18	*Clariphyllum*	3	51	1	shrub	" "	4	
19	*Jeanjacquesia*	3	8	3	cycad-like (small)	" "	6	
20	*Paraginkgo*	2	43	1	shrub	" "	3	
21	*Ctenis*	2	3	2	cycad-like (small)	" "	4	
22	*Jungites*	1	18	2	shrub or tree	" "	3	
23	*Graciliglossa*	1	13	1	slender creeper	" "	2	
24	*Cetiglossa*	1	3	1	herbaceous undergrowth	" "	2	
25	*Pagiophyllum*	1	2	1	tree	open woodland	2	1
26	*Saportaea*	1	1	1	herbaceous undergrowth	riverine forest	2	
27	*Scytophyllum*	1	1	1	shrub	" "	2	

Tab. 22. Molteno foliage genera, frequency, abundance, diversity

Arrangement: genera in order of decreasing frequency, then abundance
Frequency: number of TCs of 100 sampled in Molteno
Abundance: percentage (bold)—estimated norm in TCs yielding the genus (considering only TCs judged to represent locally growing communities)
individuals (mild)—tally of specimens in curated collection; rounded off where >50, estimate where >100
FAD score —abundance added only where 1% or more

6. THE MOLTENO BIOME

Here we consider briefly the overall floristics and vegetation of the Molteno Fm., including both the gymnospermous and non-gymnospermous elements. As elsewhere, the principal emphasis is biodiversity.

Floristics & diversity (vegetative)

The Molteno flora is the richest known in the Triassic world. As currently understood, based on a comprehensive taxonomic study of the collection (part published, part manuscript), the total vegetative diversity amounts to 57 genera and 206 species. This richness, at generic and specific level, is made up almost equally of non-gymnosperms (30 genera, 92 species) and gymnosperms (27 genera, 114 species).

Minimum:	1 genus, 1 species (as in several assemblages)	
Maximum:	37 genera, 75 species (as in Umk 111 Dic 2spp)	
Average *genera* per assemblage	(total vegetative)	: 6.81 genera
" " " "	(non-gymnosperm)	: 2.49 "
" " " "	(gymnosperm)	: 4.34 "
Average *species* per assemblage	(total vegetative)	: 9.2 species
" " " "	(non-gymnosperm)	: 2.65 "
" " " "	(gymnosperm)	: 6.44 "

Diversity per assemblage (vegetative)

The overall diversity per assemblage—based on vegetative taxa—varies considerably, ranging from a single genus and species (in several assemblages) to the uniquely rich Umkomaas site (Umk 111) with 37 genera and 75 species. The average diversity per assemblage is relatively low, at around seven genera with nine species. Although the total diversity of gymnosperms and nongymnosperms in the formation is roughly equal, there is a marked discrepancy between the two groups when the average diversity per TC is calculated. At both generic and specific level, the gymnosperms (*ca* 4.3 genera, 6.4 species) outnumber the non-gymnosperms (2.5 genera, 2.7 species) around 2:1 in average diversity.

The seven principal habitat types	species per TC (average)	TCs counted
Dicroidium riparian forest (mature)	55.5 spp	2 TCs
Dicroidium riparian forest (immature)	22.5 "	8 "
Dicroidium open woodland	9.33 "	15 "
Sphenobaiera closed woodland	14.1 "	7 "
Heidiphyllum thicket	8.0 "	18 "
Equisetum marsh	11.0 "	2 "
Fern/*Kannaskoppia* meadow	7.0 "	2 "

Habitat & biodiversity

The wide variation in diversity values is essentially an expression of the difference in floristic richness between the seven Molteno habitat types. The mature stage of the *Dicroidium* riparian forest is the richest with an average of 55.5 species per TC, and the *Heidiphyllum* thicket and Fern/*Kannaskoppia* meadow the lowest with eight and seven species respectively. Though the averages (from data as in Tab. 25) reflect a very uneven number of TCs per habitat, the figures are considered to be a fair reflection of reality.

Global diversity trends: When the Molteno diversity data are compared with global data (Niklas *et al.* 1983) through the geological column, it is obvious there is need for considerable reassessment, especially where the Triassic is concerned.

Frequency

At generic level, frequency is seen to vary greatly (Tabs 6a, 22, 23), from appearance in only one TC (*six gymnosperm genera*) to as many as 75 of the 100 TCs (*Dicroidium*). After *Dicroidium* the next most frequent genera are *Heidiphyllum* (62 TCs), *Equisetum* (50 TCs) and *Sphenobaiera* (43 TCs).

Abundance

The five most frequent genera are also the five most abundant and—apart from the fern/*Kannaskoppifolia* meadows—characterise the primary habitats (ecozones) of the Molteno Biome. Foliage genera falling in the common to abundant category range widely in frequency from *Taeniopteris* in 38 TCs down to *Dejerseya* in only five TCs. Around half of all genera fall in the rare to very rare category, i.e. fewer than 10 and five individuals respectively in most of the TCs in which they occur (Tabs 6a, 23).

Plant form

The non-gymnospermous components of the flora, as in extant vegetation, are interpreted as herbaceous plants covering a wide range of forms. Some *Equisetum* species, however, reached an impressive girth and height. The gymnosperms, on the other hand, also like their extant relatives, are seen as primarily woody. As interpreted and documented here (Tab. 23), the 27 gymnosperm foliage genera fall into the following plant-form categories: large woody shrubs to trees (11 genera), small to medium shrubs (four genera), cycad-like plants (five genera), herbaceous undergrowth (five genera), slender creepers (two genera). The proportion of woody to nonwoody gymnosperms on this count is 20:7.

Preferred habitat

The Molteno, as outlined in more detail elsewhere, was deposited on an extensive intracontinental fluvial plain. This constituted a relatively simple biome in which seven primary habitats (ecozones) have been recognised (Cairncross *et al.* 1995; Anderson *et al.* 1998). In spite of this relative uniformity, topographically, geologically and climatically, the biome supported a remarkably rich flora (and insect fauna). At generic and specific level we have explored the question of preferred habitat. From our study of all taxa across the 100 sampled TCs it is evident for many genera that each described species occupied its own relatively narrow habitat range. Excellent examples of this are clear in *Kannaskoppifolia, Batiopteris, Ginkgoites* and, on the basis of ovulate fruit, *Matatiella*.

Molteno Fm. biodiversity		
The sample: 250 000 specimens from 100 assemblages		
Observed (vegetative) .... :	206 species	
Preserved .... :	876 "	
Existed .... :	*ca* 2 000 "	
Extant southern Africa biodiversity		
(by far the world's richest temperate flora)		
Observed .... :	22 211 species	
Existing .... :	*ca* 25 000 "	nearly 10% of the world total
Extant global biodiversity		
Observed .... :	263 000 species	
Existing .... :	*ca* 300 000 "	

Biodiversity, Molteno versus extant

References: Anderson *et al.* 1996; And. & And. 1995; Anderson 1999

CLASS SUBCLASS Genera	species		fre-quency	abundance	plant form	preferred habitat
BRYOPHYTA						
Muscites		1	16			
HEPATOPHYTA						
Marchantites		9	18	very to extremely rare	mosses & liverworts	damp/shady undergrowth
INCERTAE SEDIS						
Thallites (+2 gen.)		9	6			
LYCOPHYTA						
Cylomeia (+1 gen.)		6	7		herbaceous	floodplain wetlands
SPHENOPHYTA (horsetails)						
Phyllotheca	5		6	very rare		
Schizoneura	4	21	9	common	horsetails; reed-like,	riverine and floodplain
2 genera	3		16	co-dominant	low to high	wetlands
Equisetum	9		50	monodominant		
FILICOPHYTA (ferns)						
Drepanozamites	1		2	very rare		riverine forest
11 genera	32		44	sparse		(varied)
Dictyophyllum	3	46	8	very rare	ferns	wide spectrum
Asplenites	2		4			riverine forest
miscell. (4 gen.)	8		13	extremely rare		(varied)
PINOPHYTA						
PINOPSIDA (conifers)						
Heidiphyllum	2		62	monodominant	woody (bamboo-like habit)	floodplain thicket
Clariphyllum	1	6	3	very rare	small to medium shrub	riverine forest
Rissikia	2		21	sparse	large tree	riverine & wetland
Pagiophyllum	1		1	extremely rare	tree	open woodland
CYCADOPSIDA						
Pseudoctenis	9		21	sparse		forest to woodland
Jeanjacquesia	3		3		cycad-like;	riverine forest
Ctenis	2	18	2	very rare	generally small	" "
Moltenia	4		5			" "
GINKGOOPSIDA						
Lepidopteris	2		30	sparse	medium shrub	riverine forest
Scytophyllum	1		1	extremely rare	small to medium shrub	" "
Kurtziana	16		13	rare	small tree	floodplain woodland
Dejerseya	1		5	abundant	shrub or small tree	forest to woodland
Ginkgoites	6	65	19	rare	shrub to tall tree	floodplain woodland
Paraginkgo	1		2	very rare	small to medium shrub	riverine forest
Sphenobaiera	9		43	monodominant	shrub to medium tree	lake margin
Dicroidium	19		75		shrub to large tree	forest to woodland
Kannaskoppifolia	10		26	rare	herbaceous pioneer	wide spectrum
INCERTAE SEDIS						
Batiopteris	5		10	rare	creeper	wide spectrum
Saportaea	1	6	1	extremely rare	herbaceous undergrowth	riverine forest
Linguifolium	1		9	sparse	herbaceous pioneer	water margin
BENNETTITOPSIDA						
Halleyoctenis		3	10	common	cycad-like	open woodland
Taeniopteris		8	38		shrub to small tree	forest to woodland
GNETOPSIDA						
Gontriglossa	1		8	sparse	herbaceous pioneer	water margin
Graciliglossa	1		1	very rare	slender creeper	riverine forest
Cetiglossa	1	8	1	extremely rare	herbaceous undergrowth	" "
Yabeiella	2		29	sparse	large tree	" "
Jungites	2		1	very rare	shrub or tree	" "

Tab. 23. Molteno floristics (vegetative foliage taxa), observed diversity, frequency, abundance, interpreted plant form & habitat

Non-gymnosperms: 30 genera, 92 species
Gymnosperms: 27 genera, 113 species
Total vegetative: 57 genera, 205 species

Species: based on full taxonomic review of Molteno flora
Frequency: the number of TCs in which the genus occurs
Abundance: based on scale in Tab. 8 & generalised from Tab. 6a

Plant form: as interpreted from all available clues (see And. & And., in prep., sequel to this vol.)
Preferred habitat: as interpreted from all available clues

Unnamed gnetalean (see pp. 14, 18): not included here

Primary habitats

The seven primary habitats of the extensive Molteno Floodplain Biome, each supporting a distinctive plant/insect co-association are typified as follows:

1. *Dicroidium* riparian forest (type 1): Climax, multistorey, high-diversity forest lining mature and abandoned channels crossing an earlier Triassic erosional land surface.

2. *Dicroidium* riparian forest (type 2): Preclimax, single-storey, medium-diversity forest lining shifting, braided (occasionally meandering) channels of the alluvial floodplain.

3. *Dicroidium* woodland: Low to medium-diversity woodland of the open floodplain.

4. *Sphenobaiera* woodland: medium-diversity woodland fringing lakes in the floodplain.

5. *Heidiphyllum* thicket: Monodominant to monospecific shrubby coniferous stands associated with areas of higher water-table in the floodplain, or on sandbars in the river channels.

6. *Equisetum* marsh: Monospecific horsetail stands of the floodplain marshes and lake margins, or on sandbars in the river channels.

7. Fern/*Kannaskoppifolia* meadow: Low-diversity herbaceous colonies occupying the sandbars of the braided river system.

Identifying preferred habitats

A matrix table (Tab. 24) plotting the 27 gymnosperm foliage genera against the 57 (of 100) TCs yielding fertile genera provides the basis for interpreting preferred habitats. The *taphocoenoses* (TCs) studied in the survey of a fossil flora, however, are not clean samples of plant communities like the *releves* in a phytosociological survey of an extant flora. They include a variable and incompletely understood mix of taxa from surrounding communities. With increasing knowledge of taphonomy in general and of the Molteno flora and ecosystem in particular, clarification of the autochthonous, parautochthonous and allochthonous elements of each TC will steadily improve. From the patterns of occurrence emerging in Tabs 24–28, it is possible to offer preliminary observations on habitat preferences of the whole-plant genera bearing the described ovulate structures.

A further consideration is the distinction between species and genera. It is the species, not genera, that comprise plant communities—each species within a genus having evolved to fill a different niche in the environment. Broader comment has been made in the case of *Kannaskoppia* (p. 23), a Molteno ovulate structure whose foliage is known through organic attachment. A systematic study of the foliage (And. & And., in prep.) reveals several distinct species, all interpreted as herbaceous pioneers, exploiting different habitats.

Preferred habitats of the Molteno gymnosperm taxa

The 20 Molteno ovulate genera are discussed below in the sequence followed on Tab. 26, i.e. according to their phytosociological occurrence in the seven primary habitat types.

1) ***Umkomasia***: 22 TCs, *ca* 500 individuals

Affiliation: with *Dicroidium* (Grade 4 reliability)

Species diversity: 8

Preferred habitat: *Dicroidium* riparian forest and woodland. While *Umkomasia* occurs frequently and often commonly in the three *Dicroidium*-dominated habitats, it is very infrequent and rare elsewhere.

Taphonomic filter: A number of woodland and forest TCs, though dominated by the foliage genus *Dicroidium* and well sampled (e.g. Kap 111, Maz 111, Cyp 111), yield *Umkomasia* extremely rarely or not at all. Some selective taphonomic filter must be at work. The fact that *Dicroidium* foliage often appears commonly in the *Heidiphyllum*-thicket TCs, while *Umkomasia* is virtually absent, strongly suggests that the two organs, *Dicroidium* and *Umkomasia*, are subject to different taphonomic controls, and are allochthonous elements in these assemblages.

2) ***Rissikistrobus***: 7 TCs, 85 individuals

Affiliation: with *Rissikia* (Grade 4 reliability)

Species diversity: 3

Preferred habitat: *Dicroidium* riparian forest (climax and pioneer) and less frequently *Dicroidium* woodland. The link between both *Rissikistrobus* and *Rissikia* (foliage) with *Dicroidium*-dominated TCs is very marked; even in the one *Sphenobaiera* woodland TC (Aas 411) in which *Rissikistrobus* occurs, *Dicroidium* is a dominant element.

3) ***Hamshawvia***: 4 TCs, 24 individuals

Affiliation: with *Sphenobaiera* (Grade 4/5 reliability)

Species diversity: 4

Preferred habitat: *Dicroidium* riparian forest (climax), followed by *Sphenobaiera* closed woodland.

4) ***Nataligma***: 1 TC, 4 individuals

Affiliation: with *Gontriglossa* (Grade 3 reliability)

Species diversity: 1

Preferred habitat: *Dicroidium* riparian forest (climax).

5) ***Cetifructus***: 1 TC, 2 individuals

Affiliation: unknown

Species diversity: 1

Preferred habitat: *Dicroidium* riparian forest (mature).

6) ***Alexia***: 1 TC, 6 individuals

Affiliation: unknown

Species diversity: 1

Preferred habitat: *Dicroidium* riparian forest (climax).

7) ***Hlatimbia***: 1 TC, 2 individuals

Affiliation: with *Batiopteris* (Grade 2 reliability)

Species diversity: 1

Preferred habitat: *Dicroidium* riparian forest (pioneer).

8) ***Fanerotheca***: 27 TCs, *ca* 250 individuals

Affiliation: possibly with certain species of *Dicroidium* (Grade 2 reliability)

Species diversity: 4

Preferred habitat: Occurs most abundantly in *Sphenobaiera* closed woodland and secondly in *Dicroidium* riparian forest (mature and immature). Only single specimens in four TCs have been collected in *Dicroidium* open woodland.

9) ***Fraxinopsis***: 18 TCs, 306 individuals

Affiliation: with *Yabeiella* (Grade 4 reliability)

Species diversity: 3

Preferred habitat: *Dicroidium* riparian forest (climax and pioneer) and *Sphenobaiera* closed woodland. The distribution pattern of *Fraxinopsis* is particularly clear in its frequent and common occurrence in these habitats and its near absence elsewhere.

Co-occurrence: *Fraxinopsis* links strongly with *Dordrechtites* and *Peltaspermum* and weakly with *Telemachus* and *Umkomasia*. The linkage with *Dordrechtites* possibly has to do with both genera having been wind- or water-dispersed, readily dehisced, conspicuously winged (?)megasporophylls. The occurrence of *Yabeiella* (foliage) is markedly wider in the *Dicroidium* pioneer forest and open woodland TCs than is *Fraxinopsis*. Why is the winged seed often not found in these *Dicroidium*-dominated TCs, while it is invariably preserved in the *Sphenobaiera*-dominated TCs?

10) ***Peltaspermum***: 17 TCs, *ca* 250 individuals

Affiliation: with *Lepidopteris* (Grade 4 reliability)

Specific diversity: 5

Preferred habitat: *Peltaspermum* occurs most abundantly in *Sphenobaiera* closed woodland TCs, less often in TCs of the various *Dicroidium* habitats, and rarely in those representing *Heidiphyllum* thicket. The distribution pattern of the foliage genus *Lepidopteris* (found in 30 of the 100 Molteno TCs) points clearly to the *Peltaspermum/Lepidopteris* plant being a common (never dominant), persistent element of the forest and closed woodland communities of the river bank and lake margin. The discrepancy between the foliage and fruit distributions can presumably be traced to their differing taphonomic histories.

Co-occurrence: The pattern of occurrence is most like that of *Fraxinopsis*, except in the *Dicroidium* open woodland TCs where the two genera are mutually exclusive. *Peltaspermum* and *Umkomasia*, the two most frequently occurring and abundant ginkgoopsid strobili, are often mutually exclusive. The same pattern of exclusivity is not reflected in the distribution of the foliage affiliates—*Lepidopteris* and *Dicroidium*—of the two genera. Again, some taphonomic or seasonal effect must be involved.

11) ***Dordrechtites***: 17 TCs, *ca* 400 individuals

Affiliation: unknown

Species diversity: 3

Preferred habitat: *Dordrechtites* occurs more or less equally frequently and commonly in *Dicroidium* riparian forest (climax and pioneer), *Sphenobaiera* woodland and *Heidiphyllum* thicket TCs, where the scales are presumed to be allocthonous elements. Their natural habitat is uncertain. Apart from a few fragmentary strobili, the numerous specimens occur as dehisced, wind- and/or water-dispersed, helicopter-blade ovuliferous scales.

Exclusivity: *Dordrechtites* and *Telemachus* show a distinctive mutually exclusive pattern of occurrence. Though each occurs in 17 TCs, they co-occur (highly disproportionately) in only three TCs.

12) ***Avatia***: 6 TCs, *ca* 110 individuals

Affiliation: *Ginkgoites* (Grade 2 reliability)

Species diversity: 1

Preferred habitat: *Sphenobaiera* closed woodland, where *Avatia* occurs most abundantly in the Bir 111 and Aas 411 TCs (the best sampled of the *Sphenobaiera* woodland TCs).

13) ***Fredlindia***: 3 TCs, 16 individuals

Affiliation: with *Halleyoctenis* (Grade 3 reliability)

Species diversity: 1

Preferred habitat: *Dicroidium* woodland and *Sphenobaiera* woodland. The distribution of the likely foliage affiliate, *Halleyoctenis*, corroborates these habitat preferences and points particularly to the parent plant being a relatively frequent and common component of the *Dicroidium* woodland.

14) ***Lindtheca***: 1 TC, 16 individuals

Affiliation: with *Taeniopteris homerifolius* (Grade 3 reliability)

Species diversity: 1

Preferred habitat: *Sphenobaiera* closed woodland. This very distinctive ovulate structure seemingly affiliates with *T. homerifolius*, a species that occurs quite frequently (13 TC) and commonly through the Molteno. The affiliation with *Taeniopteris*, not conclusive from the Molteno data alone, is based on knowledge of the order Pentoxylales from the Indian and Australian Lower Jurassic to Lower Cretaceous. The rarity of *Lindtheca* compared with *Taeniopteris* foliage may be a consequence of the fruit only developing every several years (as in many cycads today) and then only for a brief period.

15) ***Gypsistrobus*** 1 TC, 5 individuals

Affiliation: unknown

Species diversity: 1

Preferred habitat: *Sphenobaiera* woodland.

16) ***Avistrobus*** 1 TC, 1 individual

Affilation: unknown

Species diversity: 1

Preferred habitat: Sphenobaiera closed woodland.

17) ***Hystricia***: 1 TC, 1 individual

Affiliation: unknown

Species diversity: 1

Preferred habitat: *Sphenobaiera* closed woodland. The *Hystricia* parent-plant, was apparently a very rare and infrequent component of this lakeside woodland habitat.

18) ***Telemachus***: 18 TCs, *ca* 300 individuals

Affiliation: with *Heidiphyllum* (Grade 4 reliability)

Species diversity: 6

Preferred habitat: *Heidiphyllum* thicket. *Telemachus* occurs most frequently and commonly in this category (13 of 18 TCs), far less frequently in *Dicroidium*-dominated habitats, and is conspicuously absent from the *Sphenobaiera* woodland TCs.

19) ***Matatiella***: 4 TCs, 17 individuals

Affiliation: with *Kurtziana*, (Grade 2 reliability)

Species diversity: 4

Preferred habitat: *Matatiella*, though infrequent, appears as a distinctive species in each of four TCs representing four different habitats.

Co-occurrence: *Matatiella* almost invariably links with *Kannaskoppianthus*, such that we originally took the two genera to be female and male of the same plant. The true affiliations of the latter have since become firmly established.

20) ***Kannaskoppia***

Affiliation: with *Kannaskoppifolia* foliage (Grade 5 reliability)

Species diversity: 1

Preferred habitat: The pattern of occurrence of the genus *Kannaskoppifolia* and its several distinctive species (And. & And, in prep.) strongly points to their showing different habitat preferences. We interpret the species of *Kannaskoppifolia* as being herbaceous to twining pioneers occupying sandbanks in the braided-river, crevasse splays in the proximal floodplain, riparian-forest clearings or margins, and clearings within the *Heidiphyllum* thicket in the floodplain.

Abundance		NON-GYMNOSPERMS						GYMNOSPERMS																										
								Pinopsida				Cycadopsida				Ginkgoopsida									indet.			Be.	Pe.	Gnetopsida				
assemblages (taphocoenoses)		*Muscites*	*Marchantites*	*Thallites etc.*	lycopods	horsetails	ferns	*Heidiphyllum*	*Clariphyllum*	*Rissikia*	*Pagiophyllum*	*Pseudoctenis*	*Jeanjacquesia*	*Ctenis*	*Moltenia*	*Lepidopteris*	*Scytophyllum*	*Kurtziana*	*Dejerseya*	*Ginkgoites*	*Paraginkgo*	*Sphenobaiera*	*Dicroidium*	*Kannaskoppifolia*	*Batiopteris*	*Saportaea*	*Linguifolium*	*Halleyoctenis*	*Taeniopteris*	*Gontriglossa*	*Graciliglossa*	*Cetiglossa*	*Yabeiella*	*Jungites*
***Dicroidium* riparian forest (mature)**																																		
Umk 111	Dic 2spp	41	26	-	-	**2**	**1**	**7**	20	**5**	-	**1**	-	1	41	**1**	1	18	-	-	-	**5**	**69**	42	2	-	-	-	55	**5**	13	3	45	-
Lit 111	Dic/Hei	14	2	-	-	10	10	**23**	-	40	-	48	6	-	1	**1**	-	-	**20**	4	40	**1**	**50**	56	-	1	17	8	78	30	-	-	6	18
***Dicroidium* riparian forest (immature)**																																		
Mat 111	Dic dub	1	-	1	1	20	7	**4**	-	-	-	12	-	-	-	**1**	-	3	-	25	-	18	**89**	**2**	-	-	-	-	**2**	-	-	-	2	-
Hla 213	Dic elo	3	2	1	3	11	32	**1**	-	**2**	-	27	-	-	7	**1**	-	1	-	-	-	49	**89**	7	**2**	-	-	-	6	8	-	-	**1**	-
" 211	Dic 3spp	-	-	-	-	**10**	1	-	-	**1**	-	3	-	-	2	**1**	-	-	-	-	-	7	**85**	-	-	-	-	-	-	2	-	-	1	-
" 212	" "	-	-	-	-	**1**	6	-	-	**1**	-	**1**	-	-	4	**1**	-	-	-	-	-	7	**91**	-	-	-	1	-	5	**1**	-	-	-	-
Maz 211	Hei/Dic	2	-	-	-	7	4	**32**	1	-	-	-	-	-	-	**1**	-	-	-	3	-	**1**	**64**	-	-	-	1	-	**1**	-	-	-	11	-
San 111	Dic cra	1	-	-	-	2	1	**5**	-	-	-	1	-	-	-	**1**	-	1	-	5	3	-	**90**	3	-	-	-	-	**2**	-	-	-	**2**	-
Kap 111	Dic/Ris	-	-	-	-	**10**	4	25	30	**38**	-	40	-	-	-	2	-	-	-	-	-	20	**50**	6	-	-	4	-	3	1	-	-	5	-
Maz 111	Dic cra	-	-	-	-	**5**	3	**5**	-	-	-	-	-	-	-	2	-	-	-	1	-	**12**	**74**	-	-	-	**1**	-	-	-	-	-	22	-
***Dicroidium* open woodland**																																		
Kon 222	Dic odo	-	-	2	-	1	**1**	-	-	9	-	**3**	-	-	-	9	-	-	-	13	-	10	**87**	-	-	-	-	**8**	4	-	-	-	**1**	-
Kra 111	" "	-	-	-	1	-	**4**	-	-	-	-	-	-	-	-	10	-	4	-	-	-	1	**90**	-	-	-	-	-	**5**	-	-	-	-	-
Nuw 111	Dic zub	-	-	-	-	-	4	-	-	2	-	-	-	-	-	-	-	-	-	-	-	**30**	**70**	1	-	-	-	-	1	-	-	-	-	-
Boe 112	Dic cor	-	-	-	-	4	-	14	-	12	-	-	-	-	-	-	-	3	-	-	-	-	**99**	1	-	-	-	-	-	-	-	-	-	-
Mor 111	Dic odo	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**98**	-	-	-	-	-	**2**	-	-	-	-	-
Qua 111	" "	-	-	-	-	-	-	**20**	-	-	-	-	-	-	-	-	-	-	-	-	-	**20**	**40**	-	-	-	-	-	-	-	-	-	5	-
Gol 111	Dic dub	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**99**	-	-	-	-	-	**1**	-	-	-	-	-
Cyp 111	Dic cra	6	1	-	-	1	4	**24**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**75**	83	20	-	-	-	2	-	-	-	-	-
Ela 111	Dic odo	-	-	-	-	-	4	**7**	-	-	-	2	-	-	-	5	-	-	-	**3**	-	**1**	**87**	-	-	-	-	-	**1**	-	-	-	6	-
Pen 321	Dic/Ris	-	-	-	-	32	**5**	**1**	-	**35**	-	1	-	-	-	9	-	-	-	-	-	5	**51**	-	-	-	-	**5**	5	-	-	-	2	-
Kon 111	Dic odo	-	-	-	1	1	12	**7**	-	**2**	-	**5**	-	-	-	24	-	-	-	-	-	**5**	**78**	-	-	-	-	10	**1**	-	-	-	**1**	-
Nuw 211	Dic 2spp	-	-	-	-	-	-	**1**	-	-	-	-	-	-	-	-	-	-	-	**1**	-	3	**98**	-	-	-	-	-	-	-	-	-	-	-
Nav 111	Dic odo	-	-	-	-	-	-	**1**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**98**	-	-	-	-	-	-	-	-	-	**1**	-
Kra 311	" "	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**99**	-	-	-	-	-	-	-	-	-	18	-
Vin 111	Dic odo	1	-	-	-	-	2	**28**	-	-	-	3	-	-	-	-	-	7	-	**1**	-	4	**70**	2	-	-	-	-	4	-	-	-	-	-
Boe 111	Dic/Hei	-	-	-	-	-	-	**42**	-	-	-	7	-	-	-	-	-	-	-	-	-	-	**57**	-	-	-	-	-	**1**	-	-	-	1	-
***Sphenobaiera* closed woodland**																																		
Bir 111	Sph 2spp	40	4	7	4	20	90	**10**	-	-	-	1	1	-	-	70	-	-	-	43	-	**85**	**1**	-	1	-	-	6	70	-	-	-	40	-
Aas 411	Dic/Sph	-	5	3	50	75	24	**1**	-	25	2	19	-	-	-	**7**	-	15	-	41	-	**30**	**60**	150	-	-	-	40	**1**	-	-	-	75	-
Bir 311	Hei/Sph	-	-	-	-	-	-	**45**	-	-	-	-	-	-	-	-	-	-	-	1	-	**40**	**14**	-	-	-	-	1	-	-	-	-	-	-
" 211	Sph 2spp	1	-	-	-	-	1	3	-	-	-	-	-	-	-	-	-	-	-	3	-	**95**	**4**	-	-	-	2	-	-	-	-	-	-	-
Wal 111	Dic odo	-	-	-	-	-	-	-	-	-	-	2	1	-	-	2	-	-	-	**2**	-	**3**	**92**	-	-	-	-	-	**3**	-	-	-	20	-
Mol 111	Sph pon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**99**	12	-	-	-	-	-	-	-	-	-	-	-
Tin 121	Sph 2spp	-	-	-	-	1	-	**4**	-	1	-	-	-	-	-	1	-	-	-	-	-	**95**	**1**	-	-	-	-	-	2	-	-	-	1	-
***Heidiphyllum* thicket**																																		
Gre 121	Hei elo	-	2	-	-	20	2	**98**	-	-	-	-	-	-	-	-	-	-	**2**	-	-	-	3	22	-	-	-	-	-	-	-	-	-	-
Tel 111	" "	-	**1**	-	-	48	58	**89**	-	-	-	-	-	-	-	**1**	-	-	-	23	-	-	**6**	33	1	-	-	-	**2**	-	-	-	-	-
Kle 111	" "	-	-	-	-	**10**	-	**90**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lut 4112	Hei/Dic	-	-	-	-	-	-	**50**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**50**	-	-	-	-	-	-	-	-	-	-	-
Aas 111	Hei elo	-	17	-	-	10	**20**	**77**	-	-	-	-	-	-	-	-	-	-	-	-	-	1	7	**2**	-	-	-	-	2	-	-	-	-	-
Kan 112	" "	-	-	-	-	6	7	**98**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**1**	19	-	-	2	-	1	-	-	-	-	-
Qac 111	Hei/Dic	1	-	-	-	-	2	**50**	-	-	-	-	-	-	-	-	-	-	-	-	-	8	**50**	-	-	-	-	-	-	-	-	-	-	-
Aas 611	Hei elo	-	-	-	-	-	1	**80**	-	-	-	-	-	-	-	-	-	-	**20**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lut 111	Hei/Dic	-	-	-	-	**10**	-	**50**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**40**	-	-	-	-	-	-	-	-	-	-	-
" 511	Hei elo	-	-	-	-	-	1	**80**	-	-	-	-	-	-	-	-	-	**20**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pen 411	Hei/Dic	1	3	-	-	**2**	**3**	**94**	-	-	-	-	-	-	-	-	-	50	-	-	-	-	13	80	-	-	-	-	-	-	-	-	-	-
" 311	Hei elo	6	2	-	-	5	11	**75**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**25**	41	-	-	-	-	-	-	-	-	-	-
Kon 111	" "	-	-	-	-	**10**	-	**84**	-	-	-	-	-	-	-	-	-	**5**	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-
Aas 211	" "	10	6	-	-	-	2	**99**	-	-	-	-	-	-	-	-	-	-	14	-	-	-	-	19	-	-	-	-	-	-	-	-	-	-
" 311	" "	18	13	-	-	-	2	**99**	-	1	-	-	-	-	-	-	-	-	-	-	-	9	15	26	1	-	-	-	-	-	-	-	-	-
Win 111	" "	1	-	-	-	2	3	**79**	-	-	-	-	-	-	-	-	-	-	**10**	-	-	-	**10**	4	1	-	-	-	-	-	-	-	-	-
Lut 311	" "	6	1	-	-	30	3	**99**	-	-	-	-	-	-	-	19	-	5	-	-	-	29	58	66	-	-	-	-	23	-	-	-	9	-
Kle 111	Hei/Dic	-	-	-	-	-	-	**49**	-	3	-	-	-	-	-	**1**	-	-	-	-	-	8	**45**	-	-	-	-	-	**5**	-	-	-	-	-
Ela 112	Dic/Hei	-	-	-	-	**10**	-	**30**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**60**	-	-	-	-	-	-	-	-	-	-	-
***Equisetum* marsh**																																		
Gre 111	Equ sp	1	-	-	-	**97**	**1**	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	**2**	1	-	-	-	-	-	-	-	-	1	-
Ask 111	" "	-	-	1	-	**50**	**9**	-	-	-	-	-	-	-	-	**20**	-	-	-	-	-	**1**	**21**	-	-	-	-	-	-	-	-	-	-	-
Fern/*Kannaskoppia* meadow																																		
Kan 111	Ast spA	-	-	-	-	**22**	**63**	**10**	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	**5**	-	-	-	-	-	-	-	-	-	-
Kom 111	Sph/Dic	-	1	-	-	15	**1**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**60**	**39**	30	-	-	-	-	-	-	-	-	-	-
Uncertain habitat																																		
Boe 111	Lep sto	-	-	-	-	-	**2**	**7**	-	-	-	-	-	-	-	**90**	-	-	-	-	-	-	5	-	-	-	3	-	-	-	-	-	5	-

Tab. 24. Molteno foliage genera, abundance

Taphocoenoses (TCs): the 57 TCs are arranged as in Tab. 26
Primary habitats: see notes for Tab. 26
Non-gymnosperms: the 6 major groups encountered in the Molteno
Gymnosperm foliage genera: the 27 genera are arranged in classified sequence
Abundance: bold = % estimate made at site
mild = individuals in curated collection (where <1%)

Species diversity		NON-GYMNOSPERMS						GYMNOSPERMS																										
								Pinopsida				Cycadopsida				Ginkgoopsida									indet.			Be.	Pe.	Gnetopsida				
assemblages (taphocoenoses)		*Muscites*	*Marchantites*	*Thallites* etc.	lycopods	horsetails	ferns	*Heidiphyllum*	*Clariphyllum*	*Rissikia*	*Pagiophyllum*	*Pseudoctenis*	*Jeanjacquesia*	*Ctenis*	*Moltenia*	*Lepidopteris*	*Scytophyllum*	*Kurtziana*	*Dejerseya*	*Ginkgoites*	*Paraginkgo*	*Sphenobaiera*	*Dicroidium*	*Kannaskoppifolia*	*Batiopteris*	*Saportaea*	*Linguifolium*	*Halleyoctenis*	*Taeniopteris*	*Gontriglossa*	*Graciliglossa*	*Cetiglossa*	*Yabeiella*	*Jungites*
***Dicroidium* riparian forest (mature)**																																		
Umk 111	Dic 2spp	1	1	-	-	8	19	1	1	1	-	4	-	1	2	1	1	7	-	-	-	5	8	4	1	-	-	-	4	1	1	1	2	-
Lit 111	Dic/Hei	1	1	-	-	2	2	1	-	1	-	2	1	-	1	1	-	-	1	2	1	2	8	2	-	1	1	1	2	1	-	-	1	2
***Dicroidium* riparian forest (immature)**																																		
Mat 111	Dic dub	1	-	1	1	4	3	1	-	-	-	2	-	-	-	1	-	3	-	1	-	1	5	2	-	-	-	-	1	-	-	-	1	-
Hla 213	Dic elo	1	2	1	1	3	7	1	-	1	-	3	-	-	2	1	-	1	-	-	-	2	9	3	1	-	-	-	1	1	-	-	2	-
" 211	Dic 3spp	-	-	-	-	3	1	-	-	1	-	1	-	-	1	1	-	-	-	-	-	2	5	-	-	-	-	-	-	1	-	-	1	-
" 212	" "	-	-	-	-	1	1	-	-	1	-	2	-	-	1	1	-	-	-	-	-	1	8	-	-	-	1	-	2	1	-	-	-	-
Maz 211	Hei/Dic	1	-	-	-	1	2	1	1	-	-	-	-	-	-	1	-	-	-	1	-	1	7	-	-	-	1	-	1	-	-	-	1	-
San 111	Dic cra	1	-	-	-	1	1	1	-	-	-	1	-	-	-	1	-	1	-	1	1	-	5	2	-	-	-	-	2	-	-	-	1	-
Kap 111	Dic/Ris	-	-	-	-	4	1	1	1	1	-	1	-	-	-	1	-	-	-	-	-	1	3	1	-	-	1	-	1	1	-	-	1	-
Maz 111	Dic cra	-	-	-	-	2	1	1	-	-	-	-	-	-	-	1	-	-	-	1	-	2	6	-	-	-	1	-	-	-	-	-	1	-
***Dicroidium* open woodland**																																		
Kon 222	Dic odo	-	-	1	-	1	6	-	-	2	-	1	-	-	-	1	-	-	-	1	-	2	4	-	-	-	-	1	1	-	-	-	1	-
Kra 111	" "	-	-	-	1	-	2	-	-	-	-	-	-	-	-	1	-	1	-	-	-	1	2	-	-	-	-	-	1	-	-	-	-	-
Nuw 111	Dic zub	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	4	1	-	-	-	-	1	-	-	-	-	-
Boe 112	Dic cor	-	-	-	-	1	-	1	-	1	-	-	-	-	-	-	-	2	-	-	-	-	6	1	-	-	-	-	-	-	-	-	-	-
Mor 111	Dic odo	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	1	-	-	-	-	-
Qua 111	" "	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	1	-
Gol 111	Dic dub	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-
Cyp 111	Dic cra	1	1	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3	1	-	-	-	2	-	-	-	-	-
Ela 111	Dic odo	-	-	-	-	-	1	1	-	-	-	1	-	-	-	1	-	-	-	1	-	1	1	-	-	-	-	-	1	-	-	-	1	-
Pen 321	Dic/Ris	-	-	-	-	2	2	1	-	1	-	1	-	-	-	2	-	-	-	-	-	2	4	-	-	-	-	1	1	-	-	-	1	-
Kon 111	Dic odo	-	-	-	1	1	1	1	-	1	-	3	-	-	-	1	-	-	-	-	-	1	6	-	-	-	-	1	1	-	-	-	1	-
Nuw 211	Dic 2spp	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	1	3	-	-	-	-	-	-	-	-	-	-	-
Nav 111	Dic odo	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	1	-
Kra 311	" "	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-
Vin 111	Dic odo	1	-	-	-	-	1	1	-	-	-	1	-	-	-	-	-	1	-	1	-	1	1	1	-	-	-	-	1	-	-	-	-	-
Boe 111	Dic/Hei	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	1	-	-	-	1	-
***Sphenobaiera* closed woodland**																																		
Bir 111	Sph 2spp	1	1	3	1	1	7	1	-	-	-	1	1	-	-	1	-	-	-	2	-	2	3	-	1	-	-	1	2	-	-	-	1	-
Aas 411	Dic/Sph	-	1	2	1	1	3	1	-	1	1	4	-	-	-	1	-	1	-	1	-	2	5	1	-	-	-	1	1	-	-	-	2	-
Bir 311	Hei/Sph	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	2	2	-	-	-	-	1	-	-	-	-	-	-
" 211	Sph 2spp	1	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	1	-	2	3	-	-	-	1	-	-	-	-	-	-	-
Wal 111	Dic odo	-	-	-	-	-	-	-	-	-	-	1	1	-	-	1	-	-	-	2	-	1	2	-	-	-	-	-	2	-	-	-	1	-
Mol 111	Sph pon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3	-	-	-	-	-	-	-	-	-	-	-
Tin 121	Sph 2spp	-	-	-	-	1	-	1	-	1	-	-	-	-	-	1	-	-	-	-	-	2	1	-	-	-	-	-	1	-	-	-	1	-
***Heidiphyllum* thicket**																																		
Gre 121	Hei elo	-	1	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-
Tel 111	" "	-	1	-	-	3	3	1	-	-	-	-	-	-	-	1	-	-	-	1	-	-	4	3	1	-	-	-	2	-	-	-	-	-
Kle 111	" "	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lut 4112	Hei/Dic	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Aas 111	Hei elo	-	2	-	-	1	4	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	1	-	-	-	-	1	-	-	-	-	-
Kan 112	" "	-	-	-	-	2	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	5	-	-	1	-	1	-	-	-	-	-
Qac 111	Hei/Dic	1	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-
Aas 611	Hei elo	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lut 111	Hei/Dic	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
" 511	Hei elo	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pen 411	Hei/Dic	1	1	-	-	3	1	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-
" 311	Hei elo	1	1	-	-	1	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	3	-	-	-	-	-	-	-	-	-	-
Kon 111	" "	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Aas 211	" "	1	1	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-
" 311	" "	1	1	-	-	-	2	1	-	1	-	-	-	-	-	-	-	-	-	-	-	1	1	2	1	-	-	-	-	-	-	-	-	-
Win 111	" "	1	-	-	-	1	3	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	2	1	-	-	-	-	-	-	-	-	-
Lut 311	" "	1	1	-	-	1	1	1	-	-	-	-	-	-	-	2	-	2	-	-	-	2	3	1	-	-	-	-	1	-	-	-	2	-
Kle 111	Hei/Dic	-	-	-	-	-	-	1	-	1	-	-	-	-	-	1	-	-	-	-	-	1	4	-	-	-	-	-	1	-	-	-	-	-
Ela 112	Dic/Hei	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
***Equisetum* marsh**																																		
Gre 111	Equ sp	1	-	-	-	3	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	2	1	-	-	-	-	-	-	-	-	1	-
Ask 111	" "	-	-	1	-	3	3	-	-	-	-	-	-	-	-	1	-	-	-	-	-	2	2	-	-	-	-	-	-	-	-	-	-	-
Fern/*Kannaskoppia* meadow																																		
Kan 111	Ast spA	-	-	-	-	2	2	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Kom 111	Sph/Dic	-	1	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	2	-	-	-	-	-	-	-	-	-	-
Uncertain habitat																																		
Boe 111	Lep sto	-	-	-	-	-	2	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	1	-

Tab. 25. Molteno foliage genera, species diversity

Taphocoenoses (TCs): as for the set of tables 24–28
Primary habitats: as for the set of tables 24–28
Non-gymnosperms: the 6 major groups as in Tab. 24
Gymnosperm foliage genera: as for Tab. 24 opposite
Matrix: figures = species diversity
contrasting with abundance in Tab. 24

Phyto-sociological table				Foliage								Ovulate genera																			
				species			dominants																								
assemblages (taphocoenoses)		man-hours cleaving	♀ genera	Non-gymnos.	gymnosperms	total spp	*Dicroidium*	*Sphenobaiera*	*Heidiphyllum*	*Equisetum*	ferns	*Umkomasia*	*Rissikistrobus*	*Hamshawvia*	*Nataligma*	*Cetifructus*	*Alexia*	*Hlatimbia*	*Fanerotheca*	*Fraxinopsis*	*Peltaspermum*	*Dordrechtites*	*Avatia*	*Fredlindia*	*Lindtheca*	*Gypsistrobus*	*Avistrobus*	*Hystricia*	*Telemachus*	*Matatiella*	*Kannaskoppia*
***Dicroidium* riparian forest (mature)**																															
Umk 111	Dic 2spp	400	10	29	46	75	**69**	**5**	**7**	**2**	**1**	197	45	7	4	2	6	-	16	14	17	10	-	-	-	-	-	-	-	-	-
Lit 111	Dic/Hei	550	7	6	32	38	**50**	**1**	**23**	10	10	51	8	2	-	-	-	-	3	10	11	50	-	-	-	-	-	-	-	-	-
***Dicroidium* riparian forest (immature)**																															
Mat 111	Dic dub	65	5	10	18	28	**89**	18	**4**	20	7	75	-	-	-	-	-	-	6	-	4	-	-	-	-	-	-	-	12	6	-
Hla 213	Dic elo	60	4	15	28	43	**89**	49	**1**	11	32	32	5	-	-	-	-	2	5	-	-	-	-	-	-	-	-	-	-	-	-
" 211	Dic 3spp	4	2	4	13	17	**85**	7	-	**10**	1	3	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
" 212	" "	11	2	2	18	20	**91**	7	-	1	6	4	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Maz 211	Hei/Dic	85	5	4	15	19	**64**	**1**	**32**	7	4	46	-	-	-	-	-	-	5	63	9	40	-	-	-	-	-	-	-	-	-
San 111	Dic cra	30	5	3	16	19	**90**	-	**5**	2	1	4	-	-	-	-	-	-	5	10	2	15	-	-	-	-	-	-	-	-	-
Kap 111	Dic/Ris	65	6	5	14	19	**50**	20	25	**10**	4	2	3	-	-	-	-	-	40	26	1	-	-	-	-	-	-	-	5	-	-
Maz 111	Dic cra	30	2	3	13	16	**74**	**12**	**5**	**5**	3	-	-	-	-	-	-	-	6	27	-	-	-	-	-	-	-	-	-	-	-
***Dicroidium* open woodland**																															
Kon 222	Dic odo	40	5	8	14	22	**87**	10	-	1	**1**	22	2	-	-	-	-	-	1	-	24	-	-	3	-	-	-	-	-	-	-
Kra 111	" "	20	2	3	6	9	**90**	1	-	-	**4**	14	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Nuw 111	Dic zub	21	2	1	8	9	**70**	**30**	-	-	4	11	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-
Boe 112	Dic cor	6	2	1	11	12	**99**	-	14	4	-	8	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Mor 111	Dic odo	8	1	1	3	4	**98**	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Qua 111	" "	8	1	-	4	4	**40**	**20**	**20**	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gol 111	Dic dub	13	1	-	2	2	**99**	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cyp 111	Dic cra	100	3	4	8	12	**75**	-	**24**	-	4	2	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	5	-	-
Ela 111	Dic odo	10	4	1	8	9	**87**	**1**	**7**	-	4	1	-	-	-	-	-	-	1	-	3	-	-	-	-	-	-	-	1	-	-
Pen 321	Dic/Ris	35	2	4	14	18	**51**	5	**1**	32	**5**	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-
Kon 111	Dic odo	34	2	3	16	19	**78**	**5**	**7**	1	12	-	-	-	-	-	-	-	-	-	2	1	-	-	-	-	-	-	-	-	-
Nuw 211	Dic 2spp	6	1	-	6	6	**98**	3	**1**	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-
Nav 111	Dic odo	2	1	-	5	5	**98**	-	**1**	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Kra 311	" "	13	1	-	3	3	**99**	-	5	-	-	-	-	-	-	-	-	-	-	35	-	-	-	-	-	-	-	-	-	-	-
Vin 111	Dic odo	10	-	2	8	10	**70**	4	**28**	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Boe 111	Dic/Hei	9	1	-	8	8	**57**	-	**42**	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
***Sphenobaiera* closed woodland**																															
Bir 111	Sph 2spp	550	7	14	16	30	**1**	**85**	**10**	20	90	-	-	-	-	-	-	-	60	47	67	50	66	2	-	-	1	-	-	-	-
Aas 411	Dic/Sph	512	13	8	22	30	**60**	**30**	**1**	75	24	7	20	14	-	-	-	-	47	44	88	100	38	11	16	5	-	1	-	1	-
Bir 311	Hei/Sph	2	5	-	7	7	**14**	**40**	**45**	-	-	2	-	-	-	-	-	-	2	5	-	6	1	-	-	-	-	-	-	-	-
" 211	Sph 2spp	7	3	2	8	10	**4**	**95**	3	-	1	-	-	-	-	-	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-
Wal 111	Dic odo	50	2	-	11	11	**92**	**3**	-	-	-	-	-	-	-	-	-	-	24	12	-	-	-	-	-	-	-	-	-	-	-
Mol 111	Sph pon	4	2	-	4	4	12	**99**	-	-	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-
Tin 121	Sph 2spp	3	3	1	8	9	**1**	**95**	**4**	1	-	-	-	-	-	-	-	-	1	1	-	-	1	-	-	-	-	-	-	-	-
***Heidiphyllum* thicket**																															
Gre 121	Hei elo	10	1	3	4	7	3	-	**98**	20	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	-	-
Tel 111	" "	90	3	7	13	20	**6**	-	**89**	48	58	-	-	-	-	-	-	-	2	-	14	-	-	-	-	-	-	-	40	-	-
Kle 111	" "	15	1	1	1	2	-	-	**90**	**10**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	25	-	-
Lut 4112	Hei/Dic	2	1	-	2	2	**50**	-	**50**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	-	-
Aas 111	Hei elo	40	1	7	6	13	7	1	**77**	10	**20**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	-	-
Kan 112	" "	15	1	4	9	13	**1**	-	**98**	6	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-
Qac 111	Hei/Dic	4	1	2	3	5	**50**	8	**50**	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-
Aas 611	Hei elo	3	1	1	2	3	-	-	**80**	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-
Lut 111	Hei/Dic	2	1	1	2	3	**40**	-	**50**	**10**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
" 511	Hei elo	2	1	1	2	3	-	-	**80**	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Pen 411	Hei/Dic	70	3	6	5	11	13	-	**94**	**2**	**3**	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	50	7	-
" 311	Hei elo	35	3	5	6	11	**25**	-	**75**	5	11	3	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	17	-	-
Kon 111	" "	4	2	1	3	4	3	-	**84**	**10**	-	-	-	-	-	-	-	-	-	-	-	18	-	-	-	-	-	-	2	-	-
Aas 211	" "	35	1	3	4	7	-	-	**99**	-	2	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-
" 311	" "	100	1	4	7	11	15	9	**99**	-	2	-	-	-	-	-	-	-	-	-	-	40	-	-	-	-	-	-	-	-	-
Win 111	" "	20	1	5	6	11	**10**	-	**79**	2	3	-	-	-	-	-	-	-	-	-	-	15	-	-	-	-	-	-	-	-	-
Lut 311	" "	50	6	4	14	18	58	29	**99**	30	3	-	-	1	-	-	-	-	7	6	7	50	3	-	-	-	-	-	-	-	-
Kle 111	Hei/Dic	9	3	-	9	9	**45**	8	**49**	-	-	-	-	-	-	-	-	-	1	1	5	-	-	-	-	-	-	-	-	-	-
Ela 112	Dic/Hei	4	1	1	2	3	**60**	-	**30**	**10**	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
***Equisetum* marsh**																															
Gre 111	Equ sp	25	2	5	5	10	**2**	-	-	**97**	**1**	-	-	-	-	-	-	-	3	1	-	-	-	-	-	-	-	-	-	-	-
Ask 111	" "	14	1	7	5	12	**21**	**1**	-	**50**	**9**	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fern/*Kannaskoppia* meadow																															
Kan 111	Ast spA	30	2	4	3	7	-	-	**10**	**22**	**63**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	50
Kom 111	Sph/Dic	10	1	3	4	7	**39**	**60**	-	15	**1**	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
Uncertain habitat																															
Boe 111	Lep sto	8	1	2	5	7	5	-	**7**	-	**2**	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Total TCs												22	7	4	1	1	1	1	27	18	17	17	6	3	1	1	1	1	18	4	1

Tab. 26. Molteno ovulate genera, phytosociological table

Taphocoenoses (TCs): 57 of the 100 Molteno TCs have yielded fruit & are listed here
Primary habitats: the TCs are grouped according to the 7 Molteno habitat types; within each habitat the TCs have been shuffled to highlight phytosociological patterns
Vegetative dominants: bold & mild figures as in Tab. 24
Ovulate genera: the 20 genera are shuffled to highlight phytosociological patterns
figures = individuals in curated collection

Phyto-sociological table assemblages (taphocoenoses)	man-hours cleaving	♀ genera	Foliage: species non-gymnos.	gymnosperms	total spp	Foliage: dominants *Dicroidium*	*Sphenobaiera*	*Heidiphyllum*	*Equisetum*	ferns	Microsporangiate genera: *Pteruchus*	*Antevsia*	*Rissikianthus*	*Switzianthus*	*Helvetianthus*	*Weltrichia*	*Leguminanthus*	*Androstrobus*	*Stachyopitys*	*Cycadolepis*	*Fredianthus*	*Kannaskopp.*	*Eosteria*	*Lutanthus*	*Odyssianthus*
***Dicroidium* riparian forest (mature)**																									
Umk 111 Dic 2spp	400	10	29	46	75	**69**	**5**	**7**	**2**	**1**	138	7	8	-	-	-	-	-	19	-	-	-	-	-	-
Lit 111 Dic/Hei	550	7	6	32	38	**50**	**1**	**23**	10	10	36	4	-	50	6	2	-	-	4	-	-	9	-	-	-
***Dicroidium* riparian forest (immature)**																									
Mat 111 Dic dub	65	5	10	18	28	**89**	18	**4**	20	7	84	-	-	1	-	-	-	-	31	-	-	3	-	-	-
Hla 213 Dic elo	60	4	15	28	43	**89**	49	**1**	11	32	20	-	-	-	-	-	-	-	2	-	-	-	-	-	-
" 211 Dic 3spp	4	2	4	13	17	**85**	7	-	**10**	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 212 " "	11	2	2	18	20	**91**	7	-	1	6	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Maz 211 Hei/Dic	85	5	4	15	19	**64**	**1**	**32**	7	4	27	18	-	-	-	-	-	-	26	-	-	-	-	-	-
San 111 Dic cra	30	5	3	16	19	**90**	-	**5**	2	1	5	1	-	-	-	-	-	-	5	-	-	-	-	-	-
Kap 111 Dic/Ris	65	6	5	14	19	**50**	20	25	**10**	4	11	-	25	-	-	-	-	-	35	-	-	-	-	-	-
Maz 111 Dic cra	30	2	3	13	16	**74**	**12**	**5**	**5**	3	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-
***Dicroidium* open woodland**																									
Kon 222 Dic odo	40	5	8	14	22	**87**	10	-	1	**1**	13	2	-	-	-	1	5	-	35	10	-	-	-	-	-
Kra 111 " "	20	2	3	6	9	**90**	1	-	-	**4**	30	-	-	-	-	-	-	-	2	-	-	-	-	-	-
Nuw 111 Dic zub	21	2	1	8	9	**70**	**30**	-	-	4	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Boe 112 Dic cor	6	2	1	11	12	**99**	-	14	4	-	10	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Mor 111 Dic odo	8	1	1	3	4	**98**	-	-	-	-	1	-	-	-	-	-	-	-	30	-	-	-	-	-	-
Qua 111 " "	8	1	-	4	4	**40**	**20**	**20**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gol 111 Dic dub	13	1	-	2	2	**99**	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cyp 111 Dic cra	100	3	4	8	12	**75**	-	**24**	-	4	-	-	-	-	-	-	-	-	44	-	-	-	-	-	-
Ela 111 Dic odo	10	4	1	8	9	**87**	**1**	**7**	-	4	3	-	-	-	-	-	-	-	8	-	-	-	-	-	-
Pen 321 Dic/Ris	35	2	4	14	18	**51**	5	**1**	32	**5**	-	-	30	-	-	-	-	1	2	-	-	-	-	-	-
Kon 111 Dic odo	34	2	3	16	19	**78**	**5**	**7**	1	12	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nuw 211 Dic 2spp	6	1	-	6	6	**98**	3	**1**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nav 111 Dic odo	2	1	-	5	5	**98**	-	**1**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kra 311 " "	13	1	-	3	3	**99**	-	5	-	-	-	-	-	-	-	-	-	1	8	-	-	-	-	-	-
Vin 111 Dic odo	10	-	2	8	10	**70**	4	**28**	-	2	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-
Boe 111 Dic/Hei	9	1	-	8	8	**57**	-	**42**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
***Sphenobaiera* closed woodland**																									
Bir 111 Sph 2spp	550	7	14	16	30	**1**	**85**	**10**	20	90	-	-	-	-	-	-	-	-	113	1	-	-	5	-	-
Aas 411 Dic/Sph	512	13	8	22	30	**60**	**30**	**1**	75	24	3	-	15	2	-	-	-	-	67	3	2	21	-	1	-
Bir 311 Hei/Sph	2	5	-	7	7	**14**	**40**	**45**	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-
" 211 Sph 2spp	7	3	2	8	10	**4**	**95**	3	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Wal 111 Dic odo	50	2	-	11	11	**92**	**3**	-	-	-	-	-	-	-	-	-	-	-	21	-	-	-	-	-	-
Mol 111 Sph pon	4	2	-	4	4	12	**99**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tin 121 Sph 2spp	3	3	1	8	9	**1**	**95**	**4**	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
***Heidiphyllum* thicket**																									
Gre 121 Hei elo	10	1	3	4	7	3	-	**98**	20	2	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
Tel 111 " "	90	3	7	13	20	**6**	-	**89**	48	58	1	-	-	-	-	-	-	-	45	-	-	4	8	-	2
Kle 111 " "	15	1	1	1	2	-	-	**90**	**10**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lut 4112 Hei/Dic	2	1	-	2	2	**50**	-	**50**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aas 111 Hei elo	40	1	7	6	13	7	1	**77**	10	**20**	-	-	-	-	-	-	-	-	-	-	-	21	-	-	-
Kan 112 " "	15	1	4	9	13	**1**	-	**98**	6	7	-	-	-	-	-	-	-	-	5	-	-	5	-	-	-
Qac 111 Hei/Dic	4	1	2	3	5	**50**	8	**50**	-	2	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
Aas 611 Hei elo	3	1	1	2	3	-	-	**80**	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lut 111 Hei/Dic	2	1	1	2	3	**40**	-	**50**	**10**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 511 Hei elo	2	1	1	2	3	-	-	**80**	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pen 411 Hei/Dic	70	3	6	5	11	13	-	**94**	**2**	**3**	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-
" 311 Hei elo	35	3	5	6	11	**25**	-	**75**	5	11	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kon 111 " "	4	2	1	3	4	3	-	**84**	**10**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aas 211 " "	35	1	3	4	7	-	-	**99**	-	2	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
" 311 " "	100	1	4	7	11	15	9	**99**	-	2	-	-	-	-	-	-	-	-	-	-	-	4	12	-	-
Win 111 " "	20	1	5	6	11	**10**	-	**79**	2	3	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Lut 311 " "	50	6	4	14	18	58	29	**99**	30	3	-	-	-	-	-	-	-	-	19	-	-	16	2	2	-
Kle 111 Hei/Dic	9	3	-	9	9	**45**	8	**49**	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-
Ela 112 Dic/Hei	4	1	1	2	3	**60**	-	**30**	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
***Equisetum* marsh**																									
Gre 111 Equ sp	25	2	5	5	10	**2**	-	-	**97**	**1**	-	-	-	-	-	-	-	-	1	-	-	-	-	2	-
Ask 111 " "	14	1	7	5	12	**21**	**1**	-	**50**	**9**	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fern/*Kannaskoppia* meadow																									
Kan 111 Ast spA	30	2	4	3	7	-	-	**10**	**22**	**63**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kom 111 Sph/Dic	10	1	3	4	7	**39**	**60**	-	15	**1**	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
Uncertain habitat																									
Boe 111 Lep sto	8	1	2	5	7	5	-	**7**	-	**2**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total TCs											22	5	5	4	1	2	1	2	27	3	1	12	4	3	1

Tab. 27. Molteno microsporangiate genera, phytosociological table

Taphocoenoses (TCs): all 57 TCs as in Tab. 26 are included;
only 42 of these yield microsporangiate genera

Primary habitats: as for Tab. 26

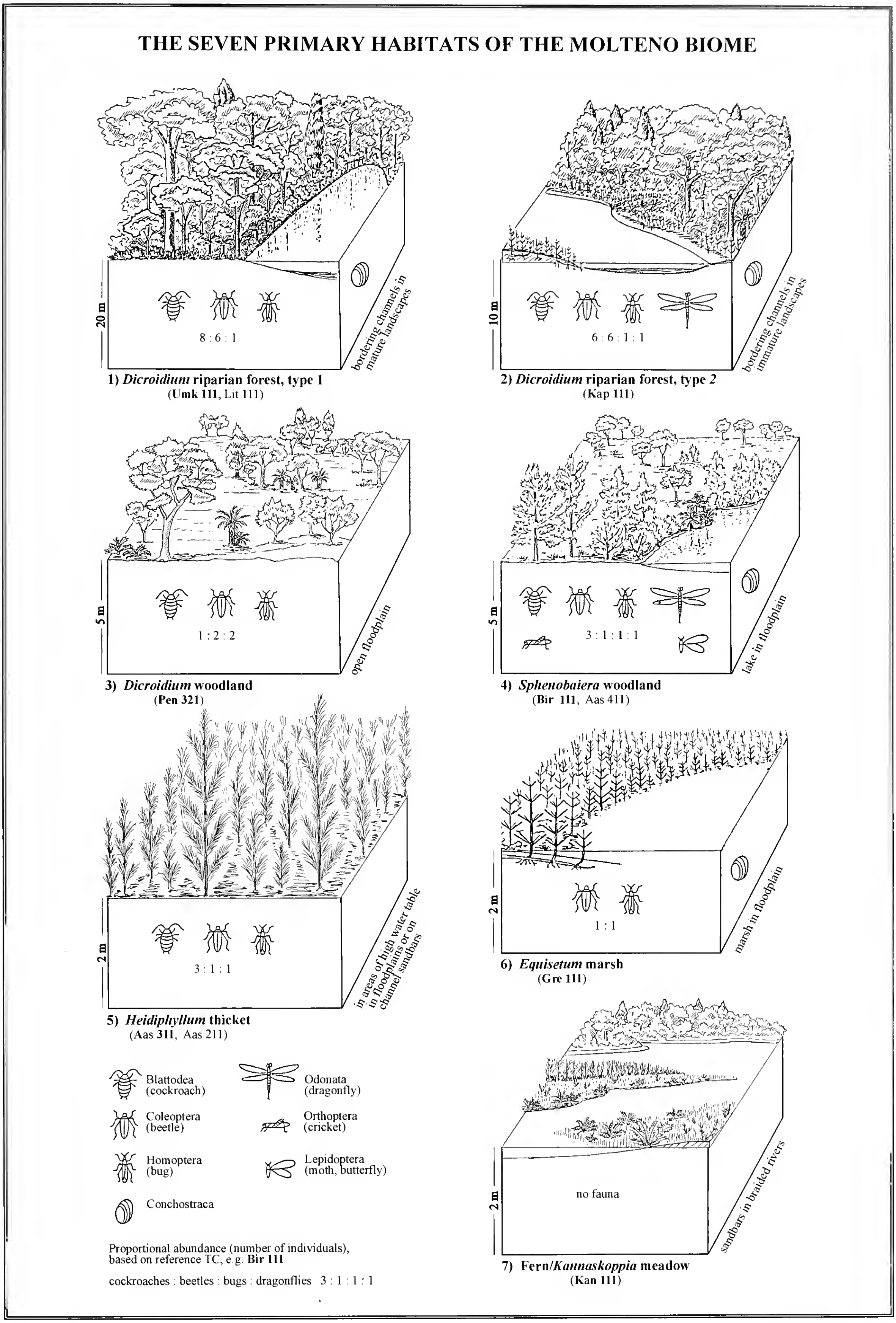
Vegetative dominants: as for Tab. 26

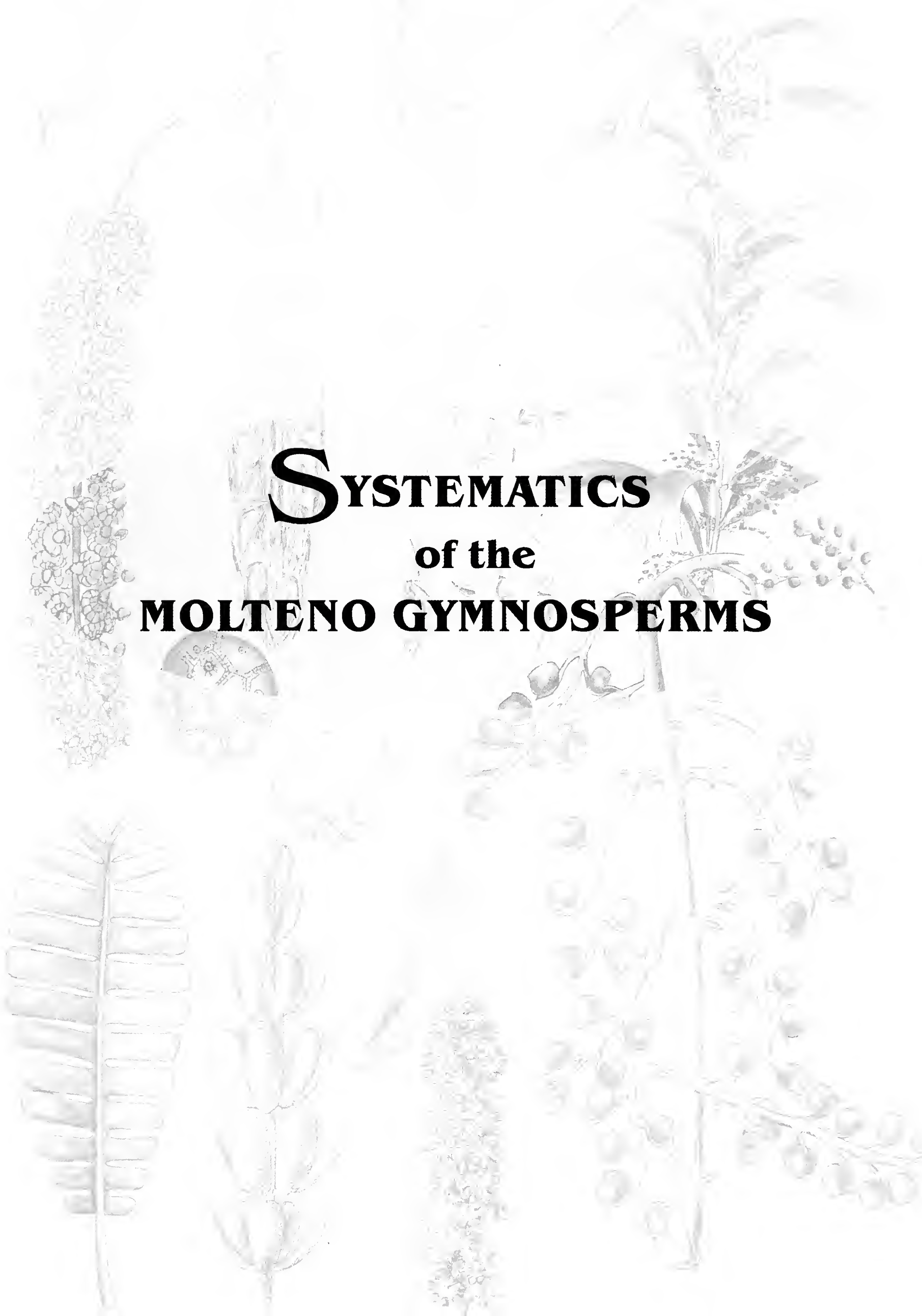
Microsporangiate genera: the 15 genera are shuffled to highlight phytosociological patterns
figures = individuals in curated collection

Species diversity	Ovulate genera																					Microsporangiate genera															
	Pinopsida					Ginkgoopsida								indet.			Be.Pe		Gnet.			Pinopsida					Cy.	Ginkgoopsida						Benn.			
assemblages (taphocoenoses)	*Dordrechtites*	*Telemachus*	*Rissikistrobus*	*Gypsistrobus*	*Avistrobus*	*Peltaspermum*	*Matatiella*	*Avatia*	*Hamshawvia*	*Umkomasia*	*Fanerotheca*	*Kannaskoppia*	*Cetifructus*	*Alexia*	*Hlatimbia*	*Hystricia*	*Fredlindia*	*Lindtheca*	*Nataligma*	*Fraxinopsis*	Total species	*Fredianthus*	*Lutanthus*	*Odyssianthus*	*Rissikianthus*	*Helvetianthus*	*Androstrobus*	*Antevsia*	*Switzianthus*	*Eosteria*	*Stachyopitys*	*Pteruchus*	*Kannaskopp.*	*Cycadolepis*	*Weltrichia*	*Leguminanthus*	Total species
***Dicroidium* riparian forest (mature)**																																					
Umk 111 Dic 2spp	1	-	3	-	-	2	-	-	2	2	1	-	1	1	-	-	-	-	1	1	15	-	-	-	1	-	-	1	-	-	2	1	-	-	-	-	5
Lit 111 Dic/Hei	1	-	1	-	-	2	-	-	1	2	1	-	-	-	-	-	-	-	-	1	9	-	-	-	-	1	-	1	1	-	1	1	1	-	1	-	7
***Dicroidium* riparian forest (immature)**																																					
Mat 111 Dic dub	-	1	-	-	-	1	1	-	-	2	1	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	1	-	2	1	1	-	-	-	5
Hla 213 Dic elo	-	-	2	-	-	-	-	-	-	3	1	-	-	-	1	-	-	-	-	-	7	-	-	-	-	-	-	-	-	-	1	3	-	-	-	-	4
" 211 Dic 3spp	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
" 212 " "	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
Maz 211 Hei/Dic	1	-	-	-	-	1	-	-	-	2	1	-	-	-	-	-	-	-	-	1	6	-	-	-	-	-	-	1	-	-	2	1	-	-	-	-	4
San 111 Dic cra	1	-	-	-	-	1	-	-	-	2	1	-	-	-	-	-	-	-	-	1	6	-	-	-	-	-	-	1	-	-	2	1	-	-	-	-	4
Kap 111 Dic/Ris	-	1	1	-	-	1	-	-	-	1	1	-	-	-	-	-	-	-	-	1	6	-	-	-	1	-	-	-	-	-	1	1	-	-	-	-	3
Maz 111 Dic cra	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	2
***Dicroidium* open woodland**																																					
Kon 222 Dic odo	-	-	1	-	-	1	-	-	-	2	1	-	-	-	-	-	1	-	-	-	6	-	-	-	-	-	-	1	-	-	2	3	-	1	1	1	9
Kra 111 " "	-	-	-	-	-	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	2
Nuw 111 Dic zub	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
Boe 112 Dic cor	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	2
Mor 111 Dic odo	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	2
Qua 111 " "	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gol 111 Dic dub	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
Cyp 111 Dic cra	-	1	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
Ela 111 Dic odo	-	1	-	-	-	1	-	-	-	1	1	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	2
Pen 321 Dic/Ris	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1	-	1	-	-	-	1	-	-	-	-	-	3
Kon 111 Dic odo	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
Nuw 211 Dic 2spp	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nav 111 Dic odo	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kra 311 " "	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	2
Vin 111 " "	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
Boe 111 Dic/Hei	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
***Sphenobaiera* closed woodland**																																					
Bir 111 Sph 2spp	1	-	-	-	1	2	-	1	-	-	2	-	-	-	-	-	1	-	-	1	9	-	-	-	-	-	-	-	-	1	3	-	-	1	-	-	5
Aas 411 Dic/Sph	1	-	1	1	-	2	1	1	1	1	1	-	-	-	-	1	1	1	-	1	14	1	1	-	1	-	-	-	1	-	3	1	1	1	-	-	10
Bir 311 Hei/Sph	1	-	-	-	-	-	-	1	-	1	1	-	-	-	-	-	-	-	-	1	5	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	2
" 211 Sph 2spp	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Wal 111 Dic odo	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
Mol 111 Sph pon	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tin 121 Sph 2spp	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	1	3	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
***Heidiphyllum* thicket**																																					
Gre 121 Hei elo	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
Tel 111 " "	-	1	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	3	-	-	1	-	-	-	-	-	1	2	1	2	-	-	-	7
Kle 111 " "	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lut 4112 Hei/Dic	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aas 111 Hei elo	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
Kan 112 " "	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	2
Qac 111 Hei/Dic	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
Aas 611 Hei elo	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lut 111 Hei/Dic	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 511 Hei elo	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pen 411 Hei/Dic	1	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
" 311 Hei elo	1	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
Kon 111 " "	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aas 211 " "	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
" 311 " "	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	2
Win 111 " "	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1
Lut 311 " "	1	-	-	-	-	1	-	1	1	-	1	-	-	-	-	-	-	-	-	1	6	-	1	-	-	-	-	-	-	1	2	-	1	-	-	-	5
Kle 111 Hei/Dic	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	1	3	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
Ela 112 Dic/Hei	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
***Equisetum* marsh**																																					
Gre 111 Equ sp	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	2	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	2
Ask 111 " "	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
Fern/*Kannaskoppia* meadow																																					
Kan 111 Ast spA	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kom 111 Sph/Dic	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
Uncertain habitat																																					
Boe 111 Lep sto	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total TCs	17	18	7	1	1	17	4	6	4	22	27	1	1	1	1	1	3	1	1	18		1	3	1	5	1	2	5	4	4	27	22	12	3	2	1	

Tab. 28. Molteno reproductive genera, species diversity

Taphocoenoses (TCs): as for Tabs 24–27
Primary habitats: as for Tabs 24–27
Ovulate & microsporangiate genera: arranged in classified sequence
Matrix: figures = species diversity
contrasting with abundance in Tabs 26 & 27


THE SEVEN PRIMARY HABITATS OF THE MOLTENO BIOME
20 m
8 : 6 : 1
bordering channels in mature landscapes
1) Dicroidium riparian forest, type 1
(Umk 111, Lit 111)
10 m
6 : 6 : 1 : 1
bordering channels in immature landscapes
2) Dicroidium riparian forest, type 2
(Kap 111)
5 m
1 : 2 : 2
open floodplain
3) Dicroidium woodland
(Pen 321)
5 m
3 : 1 : 1 : 1
lake in floodplain
4) Sphenobaiera woodland
(Bir 111, Aas 411)
2 m
3 : 1 : 1
in areas of high water table in floodplains or on channel sandbars
5) Heidiphyllum thicket
(Aas 311, Aas 211)
2 m
1 : 1
marsh in floodplain
6) Equisetum marsh
(Gre 111)
2 m
no fauna
sandbars in braided rivers
7) Fern/Kannaskoppia meadow
(Kan 111)
Blattodea (cockroach)
Coleoptera (beetle)
Homoptera (bug)
Conchostraca
Odonata (dragonfly)
Orthoptera (cricket)
Lepidoptera (moth, butterfly)
Proportional abundance (number of individuals), based on reference TC, e.g. Bir 111
cockroaches : beetles : bugs : dragonflies 3 : 1 : 1 : 1



SYSTEMATICS of the MOLTENO GYMNOSPERMS

1. FORMAT OF SYSTEMATICS SECTION

Comprehensive coverage

Reproductive element

In this systematic section we aim to present a comprehensive account to genus and species level of the gymnospermous strobili of the Molteno flora.

Vegetative element

In our two previous monographs on the Molteno gymnosperms (And. & And. 1983, 1989) we focussed on the foliage, touching only marginally on the fruit. Seven foliage genera (five new) are here added: *Scytophyllum, Kurtziana, Kannaskoppifolia* gen. nov., *Batiopteris* gen. nov., *Paraginkgo* gen. nov., *Graciliglossa* gen. nov. and *Cetiglossa* gen. nov. With these taxa, the gymnospermous foliage of the formation, at least to genus, is now also comprehensively covered.

Quality cut-off: Since our primary emphasis is taxonomic biodiversity, we have endeavoured to cover all fruiting taxa (specimens) in the collection, however rare and incompletely preserved. In the Molteno flora there exists a long tail of scarce elements represented by one or very few specimens from only one or two TCs. This is the very nature of the challenge. Even so, we must necessarily define a boundary, though imprecise, as the inclusion/exclusion cut-off. Where a specimen shows at least some unique interpretable features, allowing a meaningful line drawing or photograph, it is included and named (see also p. 49).

Seeds: Only where seeds are considered to affiliate with particular ovulate taxa are they incorporated into the body of the work. There remain many other seed types not thus accounted for. The 10 most distinctive of these appearing in the 22 most fructiferous TCs are recorded, but nowhere described, in a matrix table (Tab. 14) and plates (pls 179–152). They add to the sense of remarkable diversity in the Molteno.

Classification: We follow our own comprehensively revised '*Global classification of the gymnosperms*'—included in a sequel to this work (Anderson *et al.*, in prep.)—throughout the taxonomic account. This is based, conceptually, on the ovulate organs alone.

Organ versus whole-plant genera: In our *Prodromus of South African megafloras, Devonian to Lower Cretaceous* (And. & And. 1985), with the glossopterids (Ottokariopsida) as a core section, we followed a policy of recognising whole-plant genera and naming them after the ovulate fruit where possible. Acknowledging the cautionary arguments of authors such as Chaloner (1986), we have chosen in this volume to revert to the traditional approach of describing and naming each organ independently.

General arrangement

We have kept to a succinct, consistent and comparative layout, with the most comprehensively known whole-plant genera (e.g. *Peltaspermum/ Lepidopteris/Antevsia*) as standard. The ovulate genus is covered first, followed by the microsporangiate affiliate and lastly the foliage. The photographic plates close the treatment.

Ovulate & microsporangiate genera

All genera are treated systematically following the same essential plan. The first column of text adopts a particularly tight, synoptic framework, while the fields thereafter, from 'Reconstructions' to 'Adaptive radiation', allow for more varied treatment according to the nature of the material at hand.

Type species

The great majority of the genera and type species described here are new. Type locality, stratum and author are given for non-Molteno types.

Generic diagnosis (*or generic concept*)

We follow a general practice in extant botany where a diagnosis is a statement of those critical few characters that distinguish a taxon from adjacent taxa. It may also include geographic (e.g. Gondwana) or stratigraphic (e.g. Triassic) data to signify intent clearly and to exclude a wide scatter of uncertain material. The heading 'Generic concept' is used for previously established genera.

Generic characters

The description is intended as a succinct, systematic, comparative, morphological treatment of the reproductive genera described from the Molteno. It captures that set of diagnostic features defining the genus and separating it, in particular, from similar or related genera.

Etymology

The derivation of the name is recorded as a standard procedure.

Global range

First and last appearances are noted following the style used in our '*Global classification*' (a sequel to this work noted adjacent), which, in turn, follows '*The Fossil Record 2*' (Cleal in Benton 1993).

Gondwana Triassic (GT) occurrence

Considering the remarkable scarcity of gymnospermous fruit in the Gondwana Triassic literature, this field is more often than not limited to an entry for South Africa (Molteno). Where the genus is more widespread, comparative statistics (localities and individuals), for the other continents (regions, basins) are listed.

Molteno occurrence

A standardised documentation of frequency (F), diversity (D) and abundance (A) enables ready comparison with other ovulate and microsporangiate genera. Accompanying this is a table scoring absolute and relative abundance for the top (most productive) Molteno TCs for the particular genus.

Affiliated organs

The affiliation of organs, given central significance in describing the Molteno gymnosperms and assessing *observed* diversity, is everywhere emphasised. Reliability grades of 1 to 5, as defined on p. 16, are followed.

Classification & comparison

Two subfields are briefly discussed:

Suprageneric classification—Provides justification for placing the genus in the particular family and order chosen.

Intergeneric comparison (Gondwana Triassic)—Gives an indication of the distinctiveness of the genus, or of its similarities to the taxonomically nearest genera within the Molteno and Gondwana Triassic.

Reconstructions

Grade 4 or 5 reconstructions of the full strobilus and its diagnostic parts—for the type species and in some cases the sister species—are given. (For an outline of the grading system adopted, see p. 44.) Brief text gives a sense of the level of confidence in the reconstructions. This differs quite widely according to the quantity and quality of specimens available.

Intactness of cones

In detailing degrees of cone fragmentation, frequency of *in situ* seeds or pollen sacs, and the occurrence of dispersed scales and seeds, a sense of the proportion of immature, mature and senescent cones preserved in each taphocoenosis (TC) is given. This in turn provides clues regarding the taphonomic history from biocoenosis (living community) to taphocoenosis (death assemblage) and to the autecology of the taxon in question.

Classification (*elaborated*)

Where the morphological uniqueness and/or other attributes of a genus prompt further debate on its systematic position, we have added this field. Alternative classification schemes are discussed, as are other non-GT fossil or extant genera (in boxes) showing some similarity.

Molteno occurrence (*elaborated*)

This field is considered only for those 14 ovulate genera—*Telemachus, Rissikistrobus, Peltaspermum, Matatiella, Avatia, Hamshawvia, Umkomasia, Fanerotheca, Kannaskoppia, Hlatimbia, Fredlindia, Lindtheca* and *Nataligma*—where the foliage affiliate has been reasonably established (Tab. 12). (See further comment under 'whole-plant genera' opposite.)

Gondwana Triassic occurrence (*elaborated*)

Treatment here is particularly varied depending on (a) the extent to which the affiliation of organs has been established and (b) the frequency of occurrence of the genus beyond Africa.

Hypodigm tables (pp. 44, 45) and 'geostrat' (geographic/stratigraphic) maps (p. 45) for the Gondwana Triassic are plotted for those ubiquitous genera occurring in at least one additional continent beyond Africa.

Evidence for affiliations

As previously stressed, the whole question of affiliations is crucial to our study of floral biodiversity in the Molteno Fm. A consistent and rigorous system of grading has been employed. The evidence for applying the grades as given is documented more or less expansively according to the nature of that evidence.

Adaptive radiation

Observed species diversity, as recognised for the reproductive genera, ranges from one, for around half of all Molteno genera, to six for *Telemachus* and *Stachyopitys*, and eight for *Umkomasia* (Tab. 15). Those features that most evidently vary within the genus and serve to define the species are emphasised, as are their habitat and stratigraphic level within the formation.

Species (ovulate & microsporangiate)

As for the genera, we follow a tight comparative format in the systematic account of the species of gymnospermous fruit.

Holotype

The holotype is employed purely as a nomenclatural formality.

Reference palaeodeme (And. & And. 1985, 1989, pp. 17, 564)

It is the reference palaeodeme in our work that is core to defining the taxonomic integrity of the species. The most comprehensively sampled palaeodeme (quantity and quality of individuals) is selected as the reference palaeodeme for the species.

Sister palaeodemes (And. & And. 1989, pp. 17, 564)

Palaeodemes from the same formation (the Molteno in this case) and belonging to the same species are referred to as sister palaeodemes. A selection of the most significant examples—those most clearly adding to the understanding (morphology, cuticle, affiliations, habit, habitat, diversity etc.) of the taxon—is listed. In view of the rarity of the fruit, the majority of species do not, in fact, enjoy the backing of any sister palaeodemes.

Specific diagnosis—as for genera.

Specific characters

Only those characters found most useful in differentiating between the species of the genus are recorded. Characters uniting the species within the genus are not repeated.

Etymology—as for genera.

Comment & comparison

Here the text is confined to comparative discussion, noting diagnostic characters, habit, habitat, abundance, frequency and other attributes, as relevant, of the Molteno species included within the genus.

Foliage genera

The layout for foliage genera is largely as for the reproductive organs, except that more emphasis is given to occurrence and less to classification and species differentiation. The information is drawn largely from And. & And. (1989).

Gondwana Triassic occurrence

A comparative documentation of the prominence of each foliage genus is given through their FUDAL (Frequency, Ubiquity, Diversity, Abundance, Longevity) formulae (pp. 26, 27). This provides a measure of colonisation success.

Molteno occurrence

Since foliage is by far the most abundantly and frequently preserved of the macroscopic plant organs, it provides the standard for documenting Molteno and Gondwana occurrence.

Classification & comparison

This text is generally kept brief, with cross-reference to the '*global classification*' in a sequel (Anderson *et al*., in prep.). There the systematic relationships between taxa, as currently understood, are seen in the broadest context. In some cases, as in *Fredlindia/Halleyoctenis*, the discussion here is fuller, going beyond the scope in the later work.

Adaptive radiation

In most instances (exceptions including *Kannaskoppifolia* and *Batiopteris*), the foliage species were described in And. & And. (1983, 1989). They are not redescribed here.

Whole-plant genera

Ecological treatment of selected whole-plant genera (each on a double-page spread) is covered systematically in And. & And. (in prep.), a sequel to this work. Included are those 16 multi-organ genera in the Molteno flora (Tab. 12) where affiliation between foliage and reproductive genera (female and/or male) has been established with some degree of reliability. We find it relevant in view of our focus on floristic reality to provide a brief preview here of the scope and emphasis in the complementary monograph.

Molteno distribution patterns

A table for each whole-plant genus documents the occurrence of the affiliated organs (foliage, female and male) for each TC in which they occur. The TCs are grouped according to habitat type to facilitate comparative analysis of distributions. The patterns of co-occurrence, or the lack thereof, are seen to vary greatly. In certain instances, the female and male patterns coincide closely (e.g. *Umkomasia/Pteruchus*), in others there is no correspondence (e.g. *Kannaskoppia/Kannaskoppianthus*).

Seasonality

We attempt, considering all available clues, to reconstruct the annual (seasonal) growth cycle of the foliage and fruit (female and/or male) of each whole-plant genus. The cycle is recorded—in table and pie diagram—from immaturity through maturity to dehiscence and entombment in the deposit. A primary aim is to seek explanations for the largely discordant patterns of occurrence of the various well-established to putatively affiliated organs.

Reference taphocoenosis

The Molteno taphocoenosis in which the whole-plant genus is best represented is chosen as reference and is documented following a standard comparative scheme.

Floral association: The assemblage, documenting both vegetative and reproductive components, is listed to genus—with absolute or relative abundance. A summary of its principal characteristics follows.

Faunal association: the assemblage, primarily insects, is likewise documented—in summary table and text.

Phytosociological interpretation: An assessment of the primary and secondary plant associations (biocoenoses) as represented in the reference taphocoenosis, is attempted.

Habit reconstruction: The habit of the plant is depicted in its habitat as interpreted for the reference taphocoenosis. This is based on clues from modern analogues, taphonomy and morphology. A similar exercise was followed for the voltzialean whole-plant genus *Aethophyllum* by Rothwell *et al*. (2000).

Hla 213 depositional site: a non-aerated, abandoned channel within a braided-river system flanked by immature riparian forest on the river levee and by variously characterized meadows and thickets colonizing sandbanks within the river (below).

H/B: *Hlatimbia/ Batiopteris*: interpretation of habit, biocoenosis and depositional site.

Molteno Floodplain Biome: showing the Hla 213 depositional site within the braided river.

Pen sketches

We make extensive use of pen sketches to illustrate the Molteno gymnosperm flora. They provide the most concise interpretation of the genera and species described and of the differences and similarities between them.

Reproductive taxa: The general aim, allowing for some flexibility, has been to illustrate all species from three perspectives: a direct sketch reflecting the holotype; a full reconstruction reflecting the species; and detail sketches and/or reconstructions reflecting diagnostic parts of the cone/strobilus. In certain instances (e.g. *Helvetianthus tintinnabulum*, p. 132), additional specimens from the reference palaeodeme are drawn, while in some limited cases (e.g. *Telemachus*, pp. 86, 87) only critical elements of the holotype have been drawn.

Vegetative taxa: For foliage, the coverage is less comprehensive. Here we aim generally at a single sketch per species. For diverse genera, such as *Dicroidium* or *Sphenobaiera*, a selection of species provides an impression only of the total morphological range encountered. For established genera, the sketches are taken directly from our published monographs (And. & And. 1983, 1989), but for new taxa or those newly recognised as gymnospermous, a new range of sketches has been prepared.

Cuticles: In view of their undoubted diagnostic value at generic level, cuticle drawings have been included where possible.

Magnifications: As for photographic catalogue.

Reconstruction grades (as introduced in And. & And. 1989): All pen sketches of fossil plants are interpretive to some degree. All reflect the subjective view of the artist and/or author. In order to make the intentions of the author clear a series of reconstruction grades (R1–R5) was introduced and defined. The grade of each sketch throughout the volume is indicated.

R1: no intended reconstruction (catalogue number of individual given).

R2: minor intended reconstruction; correcting and cleaning unnecessary or ambiguous noise (minor irregularities, distortions, breaks in detail) due to imperfections of preservation or incomplete preparation; based on a single specimen (catalogue number given).*

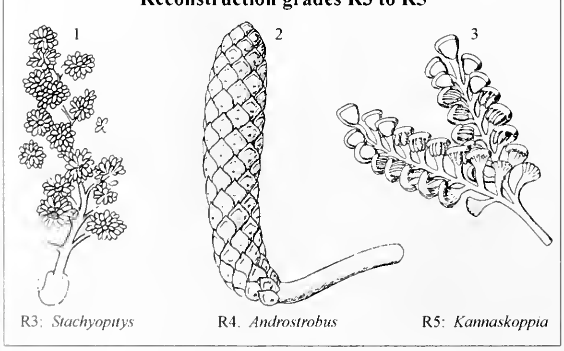
R3: intermediate reconstruction; completing or adding leaflets; based primarily on a single specimen (catalogue number given) but other members of the home palaeodeme may be consulted (assemblage code given).*

R4: extensive reconstruction (composite for palaeodeme); full frond, or other organ, reconstructed from a composite of specimens from a single palaeodeme (assemblage code given).

R5: extensive reconstruction (composite for formation); as in R4 but based on a composite of specimens from sister palaeodemes (assemblage codes given).

* Interpretations of fruit outline, diagnostic features, ornamentation etc. are based on the best preserved or most fully prepared areas of the specimen. Observations from other specimens in the palaeodeme may be incorporated to support the interpretation. The painstaking reproduction of artefact (fine-scale preservational irregularities or uncleared sediment) is misleading and ambiguous and an abdication of purpose in observation and extrapolation. A later user of the manuscript (without benefit of the original specimens) cannot know which irregularities are more real or unreal. The holotype or reference specimen is the basis for the sketch.

Reconstruction grades R3 to R5



R3: *Stachyopitys* R4. *Androstrobus* R5: *Kannaskoppia*

Photographic catalogue

Scope of catalogue

Included are a total of 152 plates with *ca* 1 500 photographs. They are dispersed through the monograph, with the plates illustrating a set of affiliated genera (whole-plant) following that group of taxa. The focus is very largely on the reproductive organs, not the foliage (see further below). New genera such as *Lindtheca* or *Fredlindia* are not favoured with greater coverage than established genera such as *Peltaspermum* or *Umkomasia*. In line with the taxonomic text, a consistent format is followed. As a rule, the more diverse the genus—the greater the number of Molteno species described—the greater the number of plates. Thus *Stachyopitys* (with six species) merits 10 plates, while *Lindtheca* (with one species) merits only two. Further factors influencing the level of coverage are morphological complexity, ornamentation and quality of preservation. The plates and line drawings are seen as complementary, the former emphasising the reality (authenticity) of the preserved specimens, the latter our interpretation of those specimens at specified grades of reconstruction.

Palaeodemes: As in our previous monographs, the plates everywhere reflect—in arrangement and captions—the palaeodeme approach, rather than individual specimens, in identifying species.

Reproductive organs: The plates comprise a comprehensive cover of the ovulate and microsporangiate genera described in this volume.

Foliage: While all leaf genera are given recognition in line drawings within the text, only those few genera (e.g. *Kannaskoppifolia*, *Batiopteris*) described here for the first time are covered, in part, photographically. The bulk of the leaf genera have been thoroughly illustrated in our earlier monographs (And. & And. 1983, 1985, 1989).

Dispersed seeds: These are covered either with their parent ovulate organs, or, for those without established affiliations (Tab. 21), on a separate set of four plates (pls 149–152) at the close of the systematic section.

Cuticles: Although cuticles have by no means been exhaustively studied for this volume (pp. 46, 47), they are illustrated where available, distinctive and instructive.

Magnifications: We adhere to a standard series of magnifications—×1, ×2, ×4 (or ×5), ×10, ×20, ×40—as with all line drawings, to facilitate comparison between taxa.

Hypodigm

Definition

The hypodigm for a given genus or species includes all the illustrated individuals (photographs or sketches), appearing in the available literature, considered here to fall within the taxon in question (And. & And. 1983, p. 226).

Scope (as applied here for the Gondwana Triassic [GT] gymnospermous fertile genera)

- A separate hypodigm table is compiled only for those GT fruiting genera that are found both in the Molteno and beyond.
- The full set of relevant GT literature appearing in the bibliography has been consulted. This comprises a remarkably limited number of references with descriptive taxonomic content. Published and reasonably accessible unpublished works (e.g. theses, survey reports) are included (indicated by a plus sign).
- Both photographs and pen sketches of all fruit specimens (hand specimens, not cuticle) are considered. Repeats are included, but are clearly indicated by an asterisk.

Purpose

The tables have wide applicability and facilitate:

- taxonomic decisions on non-Molteno taxa;
- the plotting of distribution maps for each genus and species;
- the focus of attention on assemblages and palaeodemes;
- assembling statistics on the ubiquity and frequency of taxa.

Notes on format & content of table

The design of the hypodigm tables prepared for each genus remains essentially similar, with minor changes, to that initiated for *Dicroidium* in And. & And. (1983, pp. 74, 81–87) and followed in And. & And. (1989). The changes are noted and briefly justified below.

Author: The references within each Gondwana continent are included chronologically, not by region and formation as in our earlier works. This simplification is because of the far fewer fruit illustrations (as compared to foliage) and our not attempting to circumscribe palaeodemes beyond the

Format

Molteno. Illustrations from our own previously published works on the Molteno are not recorded: these would be superfluous as the best material is all figured in the present volume.

Subregion (degree square): For a full list of the productive subregions (degree squares), with their letter and number codes spelled out and their geographic location in the Gondwana Triassic plotted, see Tab. 2, Map 1 (p. 6).

Formation: The geological formations and number codes (referring to the Standard Triassic Ammonite Zones) are shown in context in Tabs 3 and 4 (p. 7).

Locality: There still exists in the literature no generally adopted terminology or ranking in referring to the spatial occurrence of fossiliferous beds. In And. & And. (1983, p. 3), we introduced a 'locality' classification and have applied it throughout in our palaeoflora series (see Glossary). The entries in this column generally provide the most precise 'locality' data available (from all sources), but they will inevitably include 'localities' of various and unknown rank.

Name: The taxonomic names are those applied in the references cited.

Illustrations

- We refer here to plate(s) (pl) and figure(s) (f) as given in the original literature. (In this we deviate from our earlier usage [And. & And. 1983, 1989] to simplify searching the references.) The number in the left column refers to the tally of illustrated individuals as best as can be assessed.
- Where a fertile structure is refigured in a later publication, this is included but indicated as a repeat and recorded in the relevant columns by an asterisk. Here we deviate again from usage in And. & And. (1983, 1989)—where any illustrated individual was included only once—largely because of the far greater rarity of fruit. A perusal of the hypodigm still provides an immediate tally of the number of individuals illustrated for each 'locality' and species.
- Hand specimens only are included (cuticle illustrations are not considered).

Species/intactness matrix

- The species listed are the full set recognised (in this work) for the genus in the GT. They are grouped as two subsets: those recorded from the Molteno, and those recorded only beyond the Molteno.
- The illustrated specimens in the GT literature, remarkably few and mostly of poor quality, are identified as far as possible with respect to the listed set of taxa (more specifically, the reference palaeodemes defining them). Identifications are considered either 'acceptable' (1) or 'doubtful' (?1). (All digits in the matrix refer to numbers of specimens.) The poorest ('very doubtful'), individuals are included under spp. indet. The criteria adopted in defining the limits between 'acceptable', 'doubtful' (inadequate, insecure) and 'very doubtful' remain imprecise. The illustrated material currently at hand is, in general, of such a quality that it cannot bear too close a scrutiny. We await the day, not too distant, when all the best material in collections around Gondwana will be available in colour and 3D (virtual reality) to all researchers through digital photography on the Internet.
- In view of the tentative nature of many of the specific identifications, Gondwana distribution maps are plotted only for genera. All specimens included in the matrix are acknowledged on such maps.
- *Intactness.* This column, with three subcolumns—'intact strobili', 'fragmentary strobili' and 'isolated scales'—is newly added here. The purpose is to provide an easy overview of this revealing aspect of quality. Intactness is also relevant in taphonomic considerations.

Nomenclature

Taxonomy & nomenclature

In line with our practice applied throughout this volume and in our previous Molteno monographs, we differentiate clearly between specific taxa (entities) and names.

The hypodigm & nomenclature

A three-fold procedure is followed. Firstly, those entities within the Molteno considered here to be morphologically distinct at species level are recognised in the table. Secondly, any further morphological entities from elsewhere in the Gondwana Triassic considered sufficiently distinct at species level are added to the hypodigm. Thirdly, the most useful and appropriate names, following the IUCN rules of priority, are then tagged to the specific taxa.

Whole-plant genera

We refer to whole-plant genera by linking the names of the two or three affiliated organs involved, e.g. *Peltaspermum/Lepidopteris/Antevsia* or *Fredlindia/Halleyoctenis*. The female-cone name is employed first since this organ provides the primary basis for classification, the foliage name second as it is by far the most frequently and abundantly found of the organs, and the male-cone name last.

'Geostrat' distribution maps

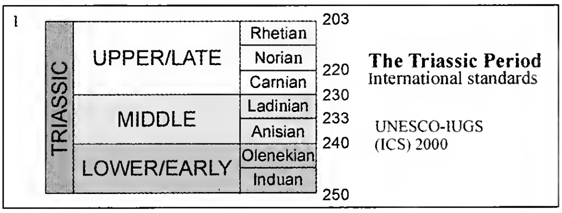
The geographic and stratigraphic distribution for the Gondwana Triassic in general and the Molteno Fm. in particular are plotted on 'geostrat' maps for each gymnosperm organ-genus—foliage, female and male—described from the Molteno. For further detail and explanation on the maps and stratigraphic table, see pp. 6–19.

Gondwana Triassic (geographic)

The geographic occurrence of genera is plotted at degree-square resolution. This affords a clear view of the currently known ubiquity of the taxa. It will be readily noted that the spread across the Gondwana supercontinent is invariably wider for the foliage genus than it is for either the female or male affiliates. It is the foliage map that gives the sense of the colonisation success of the parent genus. Distributions are based very largely on published data (solid colour in 'locality' circles), but are occasionally augmented by other sources of information on available collections or reliable on-site observations (arrow indicating open 'locality' circle, e.g. *Dordrechtites*, p. 61).

Gondwana Triassic (stratigraphic)

For convenience of comparison, we have maintained the same stratigraphic correlation chart as used in And. & And. (1983, 1989)—although knowledge of the Triassic globally has advanced significantly over the past 20 years. In particular, the latest UNESCO-IUGS (ICS) 2000 International Stratigraphic Chart (see below) plots the Triassic as spanning 47 million years from 250–203 Ma and adopts different standard stages (Induan and Olenekian) for the Lower Triassic. The correlation of plant-fossiliferous formations around Gondwana clearly needs updating, but this is not attempted for our present purpose.



Molteno Fm. (geographic)

Geographic occurrence for each of the organ-genera is plotted for the Molteno at a narrower 'superlocality' (units of 10 km diameter) resolution. This provides an intermediate-scale sense of *frequency* of occurrence. Also plotted on these Molteno maps is a degree-square grid for easy cross-reference to the Gondwana map.

2. CUTICLES

Significance of cuticles

Cuticular preparations have a significant role to play in palaeobotany and are applied here in addressing three distinct questions:

Classification: Cuticle remains strongly under-researched and under-utilised in grouping fossil gymnosperm genera at order or class level.

Molteno case study: A fine example occurs in the Fredlindiales where the cuticle, along with other morphology, shows the foliage genus *Halleyoctenis* (pp. 344, 345) to clearly exhibit proto-bennettitalean features. Several cuticular features, such as the transverse stomata, the elliptic guard cells and anomocytic (two cells) subsidiary cells, and the oblong interveinal cells with single papillae, support the comparison of *Halleyoctenis* with *Laurozamites*, an undoubted bennettitalean leaf found very commonly in the Late Triassic of the USA and Mexico. Other cuticular and macromorphological features clearly indicate the more advanced position of *Laurozamites* in the bennettitopsid clade. This becomes particularly significant when considering the fairly well-established (Grade 3) affiliation between *Halleyoctenis* and *Fredlindia*, the strikingly singular female cone from the Molteno—which is thus apparently the earliest known reproductive organ, with *Lindtheca* (p. 356) of the Bennettitopsida.

Affiliation: There exists great potential for establishing or confirming the affiliation between organs through similarities in cuticular features.

Molteno case study: *Fraxinopsis/Yabeiella* (pp. 372–377) provides a convincing example in that *Yabeiella* (foliage) and *Fraxinopsis* (female fruit) yield cuticle with more or less identical and uniquely characteristic features. The nonpapillate amorphous cells with meandering walls together with the anomocytic (4–6 cells), noncutinised subsidiary cells and narrowly elliptic guard cells to the stomata, characterise both *Yabeiella* and *Fraxinopsis*. Only *Jungites* (foliage) placed in the same family has similar cuticle. The affiliation between *Yabeiella* and *Fraxinopsis* was previously well established on the basis of mutual occurrence, but the cuticle adds powerful confirmation.

Habit & habitat: Robustness of cuticle, differences between upper and lower cuticle, presence of papillae and/or lappets, and stomatal frequency, may lend clues to growth form and autecology, including climatic factors (And. & And. 1983, pp. 52, 53).

Molteno case study: A particularly engaging cuticular feature is found to characterise the two most diverse and often dominant Gondwana Triassic foliage genera, *Dicroidium* (p. 256) and *Sphenobaiera* (p. 222). Both show a full range from distinctly linear to broad-leaved species. And in each there is clearly witnessed a parallel range in the cuticle from fully amphistomatic (narrow-leaved forms), with equal stomatal density in the upper and lower cuticle, to fully hypostomatic (broad-leaved forms), with high stomatal density in the lower cuticle but no stomata in the upper cuticle. The hypothesis, as outlined in And. & And. (1983, 1989) and developed further in a sequel to the present work, is that the narrow-leaved forms of both genera occurred as dominant trees in the open woodland of the Molteno floodplains, while the broad-leaved forms grew as undershrubs in the closed forest lining the braided rivers.

Molteno sampling

The great majority of the 100 sampled Molteno taphocoenoses (assemblages) yield specimens preserved as impressions (occasionally moulds and/or casts); only a few yield compression material with cuticle. The two assemblages Little Switzerland (Lit 111) and Umkomaas (Umk 111) have provided by far the most excellently preserved cuticle and, fortuitously, are also the most diverse Molteno assemblages, with 39 and 73 vegetative species respectively.

In Tab. 29, we record those female-fruit genera, with abundance data, occurring at Lit 111 and Umk 111. Also shown are the supposed foliage and male-fruit affiliates of these genera, again with abundance data for Lit 111 and Umk 111. The cuticles of all the foliage genera have been fully described in And. & And. (1989), while those of the female and male fruit are prepared and described in this volume with a view to answering, where feasible, the three questions noted above. The table gives a clear indication of the potential in this regard: fully half (10 of 20) of the female-fruit genera are known from at least one of the two localities; a higher tally of female/foliage affiliates (14 of 20 genera) occurs at Lit 111 and/or Umk 111; while the tally of female/male-fruit affiliates (5 of 20 genera) is markedly lower.

Where the cuticle of a reproductive genus has been previously studied, i.e. *Rissikistrobus*, *Peltaspermum*, *Umkomasia* and *Pteruchus* by Thomas (1933) and/or Townrow (1960, 1962, 1965, 1967), we have not dedicated time to repeating the research.

Alternative methodologies

Four methods have been followed here, however cursory, in studying the epidermal features of the Molteno fruit:

a) Conventional maceration.
b) Acetate peels—compression material, where maceration fails (e.g. for *Fraxinopsis/Yabeiella*, pp. 370–383).
c) Acetate peels or direct light microscopic observation—fine-grained impression material (e.g. *Lutanthus ornatus* pollen sacs, p. 77, pl. 80).
d) Jed Scanning Microscope—compression or impression material, small hand specimens, where all else fails (e.g. *Dordrechtites*, p. 63).

Cuticle features

All descriptions of cuticular morphology follow the terminology outlined in detail in And. & And. (1989, pp. 58–61).

Cuticle grade

The quality of the cuticle differs widely for the different genera: from *very poor* (no features discernible) in *Nataligma* to *excellent* (most features clearly preserved) in *Hamshawvia*. A scale of five grades (developed in And. & And. 1989, pp. 54, 55) is applied.

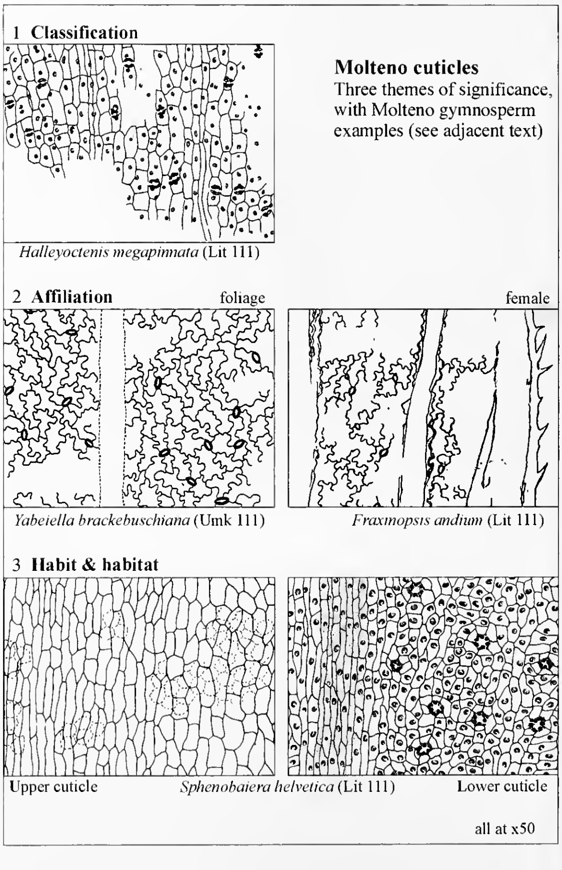
Preservation grades (as in And. & And. 1989)

1. *v. poor*—cuticle (&/or mesophyll tissue) definitely present, but aside from veins, shows no interpretable structures (cell walls, stomata).
2. *poor*—minimal interpretable structures (besides veins).
3. *fair*—intermediate preservation, generally very fragmentary, a few interpretable features, LM photography passable.
4. *good*—most features visible, LM and SEM photography suitable.
5. *v. good* (excellent)—features very clear, large pieces available, LM and SEM photography admirably suitable.

Notes

(a) The same system of grades is applied to individual specimens and to assemblages (Tab. 29). In the case of assemblages, the grade given refers to the best preserved taxa (i.e. ginkgoopsids).

(b) Precision in applying grades is difficult since we are dealing with a continuous scale involving assorted variables: general preservation, clarity of specific features, size of cuticle fragments.



Molteno cuticles
Three themes of significance, with Molteno gymnosperm examples (see adjacent text)

	Female ♀	Lit 111		Umk 111		Foliage	Lit 111		Umk 111		Male ♂	Lit 111		Umk 111	
1	*Dordrechtites*	50	✓2	10	-	-	-	-	-	-	-	-	-	-	-
2	-	-	-	-	-	-	-	-	-	-	*Fredianthus*	-	-	-	-
3	-	-	-	-	-	-	-	-	-	-	*Lutanthus*	-	-	-	-
4	*Telemachus*	-	-	-	-	*Heidiphyllum*	**23%**	✓3	**7%**	✓3	*Odyssianthus*	-	-	-	-
5	-	-	-	-	-	*Clariphyllum*	-	-	20	✓1	-	-	-	-	-
6	*Rissikistrobus*	10	-	45	*	*Rissikia*	40	✓1	**5%**	✓3	*Rissikianthus*	-	-	8	-
7	-	-	-	-	-	*Pagiophyllum*	-	-	-	-	-	-	-	-	-
8	*Gypsistrobus*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	*Avistrobus*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10	-	-	-	-	-	-	-	-	-	-	*Helvetianthus*	6	✓5	-	-
11	-	-	-	-	-	*Pseudoctenis*	48	✓2	**1%**	✓1	*Androstrobus*	-	-	-	-
12	-	-	-	-	-	*Jeanjacquesia*	6	✓3	-	-	-	-	-	-	-
13	-	-	-	-	-	*Ctenis*	-	-	1	✓2	-	-	-	-	-
14	-	-	-	-	-	*Moltenia*	1	✓1	41	✓3	-	-	-	-	-
15	*Peltaspermum*	12	-	17	*	*Lepidopteris*	**1%**	✓5	**1%**	✓4	*Antevsia*	4	-	7	-
16	-	-	-	-	-	*Scytophyllum*	-	-	1	✓3	-	-	-	-	-
17	*Matatiella*	-	-	-	-	*Kurtziana*	-	-	18	✓3	-	-	-	-	-
18	-	-	-	-	-	*Dejerseya*	**20%**	✓5	-	-	*Switzianthus*	50	✓5	-	-
19	*Avatia*	-	-	-	-	*Ginkgoites*	44	✓5	-	-	*Eosteria*	-	-	-	-
20	-	-	-	-	-	*Paraginkgo*	40	✓5	-	-	-	-	-	-	-
21	*Hamshawvia*	2	✓4	7	✓3	*Sphenobaiera*	**1%**	✓5	**5%**	✓5	*Stachyopitys*	4	-	19	-
22	*Umkomasia*	50	-	100	*	*Dicroidium*	**50%**	✓5	**69%**	✓5	*Pteruchus*	35	-	100	*
23	*Fanerotheca*	3	-	30	✓3	*Dicroidium*	-	-	-	-	-	-	-	-	-
24	*Kannaskoppia*	-	-	-	-	*Kannaskoppifolia*	51	✓4	42	✓4	*Kannaskoppianthus*	9	✓3	-	-
25	*Cetifructus*	-	-	2	-	-	-	-	-	-	-	-	-	-	-
26	*Alexia*	-	-	6	✓3	-	-	-	-	-	-	-	-	-	-
27	*Hlatimbia*	-	-	-	-	*Batiopteris*	-	-	2	✓2	-	-	-	-	-
28	*Hystricia*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
29	-	-	-	-	-	*Saportaea*	1	✓2	-	-	-	-	-	-	-
30	-	-	-	-	-	*Linguifolium*	17	✓3	-	-	-	-	-	-	-
31	*Fredlindia*	-	-	-	-	*Halleyoctenis*	8	✓3	1	✓1	*Cycadolepis*	-	-	-	-
32	"	-	-	-	-	"	-	-	-	-	*Weltrichia*	1	-	-	-
33	-	-	-	-	-	-	-	-	-	-	*Leguminanthus*	-	-	-	-
34	*Lindtheca*	-	-	-	-	*Taeniopteris*	78	✓3	55	✓1	-	-	-	-	-
35	*Nataligma*	-	-	3	-	*Gontriglossa*	30	✓3	**5%**	✓2	-	-	-	-	-
36	-	-	-	-	-	*Graciliglossa*	-	-	13	✓1	-	-	-	-	-
37	-	-	-	-	-	*Cetiglossa*	-	-	3	✓1	-	-	-	-	-
38	*Fraxinopsis*	10	✓3	12	-	*Yabeiella*	6	✓1	45	✓3	-	-	-	-	-
39	-	-	-	-	-	*Jungites*	18	✓3	-	-	-	-	-	-	-
	20 genera	7		10		27 genera	19		19		15 genera	7		4	

Tab. 29. Cuticle potential in the Molteno (Lit 111 & Umk 111)

Genera: in classified order reflecting affiliations (see Tab. 13, p. 19)
Female: 10 of 20 Molteno ovulate genera occur at Lit 111 &/or Umk 111
Male: 8 of 15 Molteno male "
Foliage: 26 of 27 Molteno foliage "

In the locality columns, the first figure gives the number of curated specimens (or % abundance in the case of foliage) whilst the second gives cuticle grade.

Bold figures: % estimate made at site
Mild figure: individuals in curated collection (where <1%)

✓: cuticle (grade 1—5 preservation) prepared by HMA (this vol., or our previous vols.)
* : cuticle prepared by Townrow (1960, 1962, 1965, 1967) &/or Thomas (1933)

3. TAXONOMIC GUIDELINES

Like justice, palaeobotany is an inexact science. And, as in justice, it is necessary to seek terms and concepts to reflect the inexactness and to guide our methodology towards reaching the best approximation of the truth. Below follows a scheme of the guidelines adopted—much of which might sound self-evident, yet is not so. Divergent views on palaeobotanical—indeed all palaeontological—taxonomy, at all ranks from class to species (and below), have coloured our science for decades and remain extreme. There is no agreed methodology, there are few agreed guidelines. Nor is there any sense that current differences might be narrowing. If we are to track biodiversity patterns through geological time successfully, convergence of approach will be a key necessity.

Seeking the holistic truth (reality): the primary guiding principle

- '*Deep ecological awareness recognizes the fundamental interdependence of all phenomena . . .*'—Fritjof Capra, *The web of life* (1996).
- What was the holistic reality of life—plants, animals, landscape, climate—back in Molteno times in the Late Triassic (*ca* 200 Ma)?
- Taxonomic entities, at all levels, from species and genera to families, orders and classes, are defined with the biological reality always uppermost in mind.
- Form taxa, basket taxa, morphospecies and related pragmatic concepts are therefore avoided wherever possible.

Biodiversity, paleoecology, biogeography, phylogeny

- These are the themes that drive our Molteno research.
- Taxonomy provides the fundamental data essential to exploring these themes.
- Consistent and rigorously derived taxonomy will underscore sound hypotheses concerning biodiversity and paleoecology.
- Inconsistent, variously derived taxonomy, will undermine hypotheses concerning biodiversity and paleoecology.

Nothing by mere authority ('*Nullius in verba*')

- This is the motto of the British Royal Society, instituted in England in 1660 to promote scientific research and discussion.
- The motto encourages observation and experiment before precedent and authority.
- Newer, more complete data supersede historic, less complete data.
- Resolution of a dispute is often best resolved by collecting more data.

Beyond our time & space

- To maintain objectivity, to build in hindsight, visualise making taxonomic and related decisions from a vantage point outside your current framework of reference in time and space. Imagine yourself looking back critically at your own work—not as a peer reviewer, but as a descendent-generation reviewer—from 100 years in the future and from the opposite hemisphere.
- Consider those making taxonomic decisions early in the 20th century doing likewise. How might this have coloured their approach and their results?

Further on holism & the interdependence of all phenomena

- The '*Unity of knowledge*' (Wilson 1998) is the framework in which the Molteno details are assessed.
- All clues are relevant and synergistic.
- 'Holistic thinking' is not 'circular thinking'.

Contextual thinking

- When studying the taxonomy of the Molteno, we are fully aware that temporally we are exploring life within the Late Triassic and not, for instance, the Late Devonian or Late Permian. And we are cognisant that geographically we are dealing with Gondwana and not Pangaea as a whole.
- We have in mind from our own previous work (And. *et al.* 1996, 1999a) that we are very probably working within a time of peak diversity; near the height of the 'Triassic explosion of diversity', and very close to, if not coinciding with, the 'heyday of the gymnosperms'.

Superficial similarities at generic & higher level

- Is a *Glossopteris*-like leaf found in the Late Triassic a *Glossopteris*? Is a *Ginkgo*-like leaf from the same strata a *Ginkgo*, or a *Podozamites*-like leaf a *Podozamites*?
- This is a perennial problem and a crucial one—involving both morphological (including affiliations) and contextual considerations.
- Consider *Gontriglossa* (p. 364) and *Glossopteris*, for example: contextually, such taxa are less likely to be congeneric, confamilial or conordinal if separated in time by one or more of the five major global extinction events, the end-Permian in this case.

Superficial similarities at specific & generic level

- Are three widely distinct *Glossopteris*-like species in the Late Triassic congeneric or more likely representatives of three distinct genera (see *Gontriglossa, Graciliglossa* and *Cetiglossa*; pp. 364–369)?
- This, again, is a constant problem and one that demands a solution involving both morphology and context.
- Were these taxa from the Gondwana Permian, they would automatically be considered congeneric, i.e. *Glossopteris*.
- Contextually, such taxa are less likely to be congeneric if found in the Late Triassic (at the peak of diversity) than if found in the Early Triassic (at the trough of diversity).
- Proof of congeneric status will most likely depend on well-established fruit (female and/or male) affiliations, and/or clear and unique cuticular conformity; and/or obvious similarity in mode of attachment.

Habitat & conspecificity

- The recognition of habitats/ecozones within the Molteno introduces a further parameter in species-level taxonomy.
- A taxonomic law that generally holds in the extant world is that distinct species within a genus occupy distinct habitats; or conversely, any one habitat is unlikely to harbour more than one species of the same genus.
- Palaeodemes of a particular genus deriving from a number of clean/uncontaminated/unambiguous TCs representing a distinct habitat are more likely than not to represent a particular species.

Virtual reality (today is the key to the past)

- Imagine traversing the habitats of the Molteno Biome at the time they thrived. Walk those woodlands and riverine forests of the Late Triassic as if you were walking their equivalents today. Feel their ecology and biodiversity, conceive the interaction between plant, insect and vertebrate species. Live those communities comprising biological species just as today.
- Taxonomy and Late Triassic floristics will mirror reality more closely as the virtual reality landscape comes into more vivid focus. Past reality and present study merge in harmony.

Optimal sampling

- Optimal sampling of a formation will increase the chances of making optimal taxonomic decisions.
- The more intensive/extensive the sampling of a fossiliferous formation, the higher the proportion of correct decisions—all else being equal.
- When in doubt, increase the collection.

Curation & the palaeodeme approach

- The palaeodeme (population) approach—or something akin—is considered obligatory if the taxonomic goal is to approximate the original living reality (pp. 22–25). Curation emphasising palaeodemes and taphocoenoses will maximise taxonomic reliability.
- Optimal curation involves the facilities necessary for the study of several palaeodemes simultaneously for comparative study. Moveable trays (with many specimens showing variation within a palaeodeme) and a closely adjacent, generously spacious, working surface on which to display an array of trays are pivotal.

Preparation & morphological data

- Dedicated preparation of specimens will optimise the proportion of correct taxonomic decisions.
- Cleanly exposing (chipping clear) a range of individuals within a palaeodeme proves invaluable.
- Cuticular preparations and anatomical sections add to the inventory of comparative data.

Objective & interpretive illustration

- Photographs (objective representations) and sketches (the authors' faithful interpretation of morphology) of the best individuals covering a palaeodeme are worth more than the proverbial plethora of words.

The lower cut-off

- It is in the nature of palaeobotany, no matter how small or large the collection, that the rarer taxa and/or organs are more likely to be represented by poorer quality specimens.
- Where biodiversity is a core theme—as in this work—this innate problem has to be faced more emphatically than otherwise. Exacerbating the problem is that in richer fossil floras (or insect faunas) a high proportion of species appear both very rarely and very infrequently (pp. 20–25). The more diverse the flora, the longer this tail.
- The lower cut-off in the quality of individuals accounted for in erecting new taxa is necessarily lowered for rarer taxa.
- Specimens below the lower cut-off are those that are simply too inadequate for identity.
- Adequacy—an elusive measure—depends on the ability to see, sketch or photograph definable diagnostic features on which the taxon can be based (subjectivity is unavoidable).

The cone of uncertainty

- Uncertain decisions permeate palaeobotany; they are unavoidable and are the very fabric of our research.
- All taxonomic decisions—including affiliations—are hypotheses (concepts), some more sound than others.
- Such decisions range from near certain to distinctly uncertain, but they cannot be avoided (assuming the material at hand falls above the nominated lower cut-off).
- Certainty increases with more material.
- Uncertainty increases with less material.

Controversial decisions (unanimity, mutuality, veto)

- The further down the cone of certainty-uncertainty, the less likely unanimity will be reached.
- A veto rule has been applied in cases where a split vote has occurred between ourselves (HMA and JMA) on a controversial decision.
- After due debate, each author secretly records his/her percentage vote for a particular yes-no decision. (The votes 'for' may turn out to be as decisive as 70–30% or as unsure as 49–51%). The average of the votes of the two parties will be the decider. Further lobbying of viewpoints may intervene before settlement.

  Candidly documenting (and scoring) particularly uncertain decisions (divergent votes) in a manuscript might prove valuably revealing, e.g. JMA 70–30% for two particular species being congeneric; HMA 49–51% against the two species being congeneric.

The balance of probability

- In the conventional 'Criminal Justice System', the particularly rigorous guideline of 'proof beyond reasonable doubt' is employed: a person is 'innocent unless proved guilty'. Even so, miscarriages of justice do occur.
- In palaeobotany, were this rigorous guideline introduced, very few taxonomic decisions—at any level from species to class—would ever be taken. We would emerge with a soup of words, but no taxa.
- The recent Truth and Reconciliation Commission in South Africa adopted the far less rigorous 'balance of probability' measure in assessing the truth of a person's testimony.
- This 'balance of probability' is the guideline underscoring much of our palaeobotanical taxonomy.

4. MORPHOLOGICAL TERMINOLOGY

In the four-page spread that follows we present an illustrated key with the aim of capturing all critical or specialised terminology used here in describing the gymnospermous reproductive structures of the Molteno. While there is no absolute consensus on usage in the more recent literature, we have endeavoured to stay with the majority. We have therefore shifted from our *Prodromus of South African fossil floras* (And. & And. 1985) in which we chose to adopt the terms—such as fertiliger and polysperm—introduced by Meyen (1987) specifically for gymnosperms.

No attempt has been made to include all Molteno fruiting genera comprehensively, as long as the key comparative morphology and terms are covered. And for certain groups, to promote further clarity, non-Molteno material is added. Pen sketches of the latter are included in a box with geographic and stratigraphic sources indicated.

The key serves also to summarise our interpretations of analogous and homologous organs.

Analogous: organs or parts having the same function but different evolutionary origin, e.g. paddle of whale and fin of fish; convergent evolution.

Homologous: organs or parts having the same evolutionary origin, but different functions, e.g. paddle of whale and wing of bat; divergent evolution.

Ontogenetic variation (series, developmental stages)

Analysis of ontogenetic level—immature to senescent—at fossilisation can reveal interesting information on a range of related issues: taphonomy, affiliation, seasonality, diversity.

Cone buds—not found in the Molteno.

Immature (or abortive) *cones*—very rarely encountered in the Molteno, e.g. *Dordrechtites*, 1 specimen (p. 64, tf. 9) from Lutherskop, and *Hamshawvia*, a single strobilus from Aasvoëlberg found attached to a short shoot with *Sphenobaiera* leaves (pp. 210, 229).

Mature cones—with scales, bracts, seeds and pollen sacs (with *in situ* pollen) intact; a small proportion of Molteno material, e.g. *Rissikianthus concavus*, a fine palaeodeme of shed cones with *in situ* microsporangia (p. 109) from Peninsula, and *Kannaskoppia vincularis*, a unique palaeodeme of strobili including a good many found attached to fragments of shoot with or without *Kannaskoppifolia* leaves (pp. 288, 289).

Senescent cones—with scales, bracts, seeds, pollen sacs and pollen shed or dehisced to lesser or greater degree; the great majority of Molteno reproductive material falls in this category, e.g. *Dordrechtites* (pp. 60–69), frequent and abundant in the Molteno, but almost exclusively found as dehisced ovuliferous scales, and *Kannaskoppianthus* (pp. 290–293), with virtually all strobili found detached and the great bulk having shed their pollen sacs.

Strobilus

The term is used here generally for all gymnospermous male and female reproductive organs, whether bearing compact or distantly spaced sporophylls.

We use the following terms for different basic types of strobili:

Cone: radially symmetrical compact strobili with imbricate or adjoining scales—as for most female and male pinopsids (e.g. *Telemachus*, *Odyssianthus*).

Pinnate or bipinnate ovulate 'paniculate' lamina: dorsiventral, bilaterally symmetrical, laminate strobili, reminiscent of fertile fern fronds—as for certain female ginkgoopsids (e.g. *Umkomasia*, *Kannaskoppia*).

Lax infructescense: 'catkin'-like strobili with irregularly helical arrangement of microsporangial heads—as for certain male ginkgoopsids (e.g. *Pteruchus*, *Stachyopitus*).

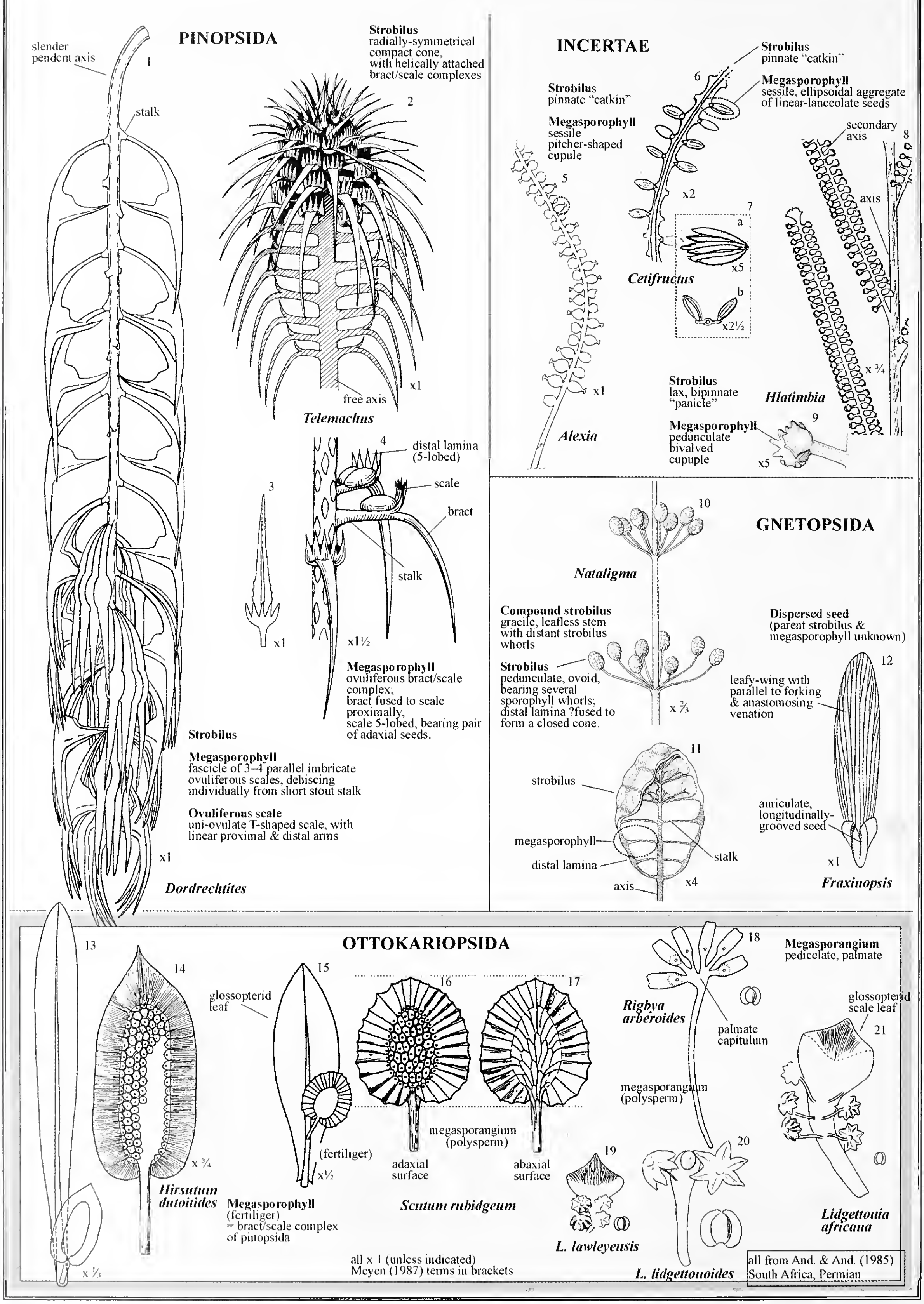
Ottokariopsida (glossopterids)

On both the female and male spreads, we include a panel showing a range of glossopterid reproductive structures, though the class of plants remains unknown in the Molteno.

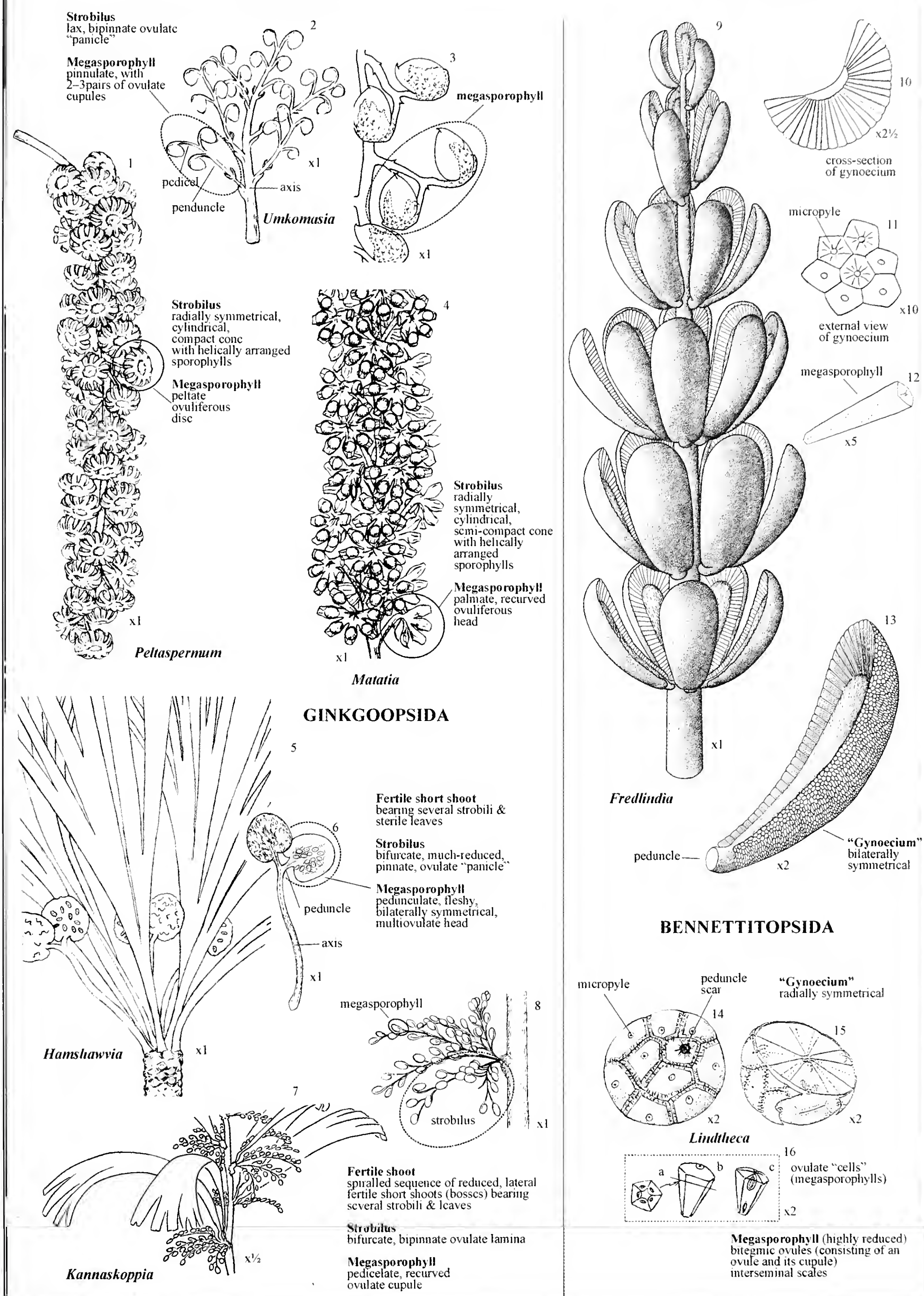
As recognised by various authors (White 1986; Retallack & Dilcher 1988; Anderson *et al.* 1999a), the glossopterids, absolutely dominant through the Gondwana Permian and heavily decimated at the end-Permian extinction, appear to have been a veritable nursery for new orders of gymnosperm (and possibly stem angiosperms) that arose during the extraordinary radiation of new life through the Triassic.

In discussing the phylogeny and classification of the Molteno genera, therefore, we make regular reference back to their possible ancestral glossopterid lineages.

MORPHOLOGICAL TERMINOLOGY: female strobili

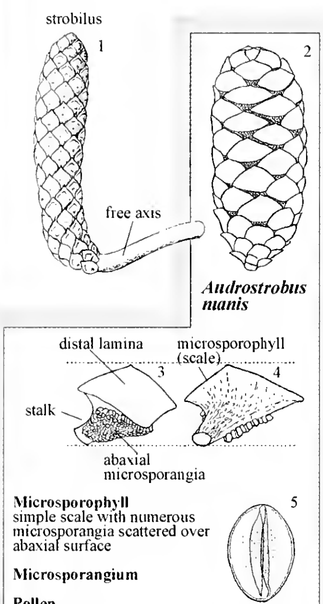


MORPHOLOGICAL TERMINOLOGY: female strobili



MORPHOLOGICAL TERMINOLOGY: male strobili

CYCADOPSIDA



Microsporophyll
simple scale with numerous microsporangia scattered over abaxial surface

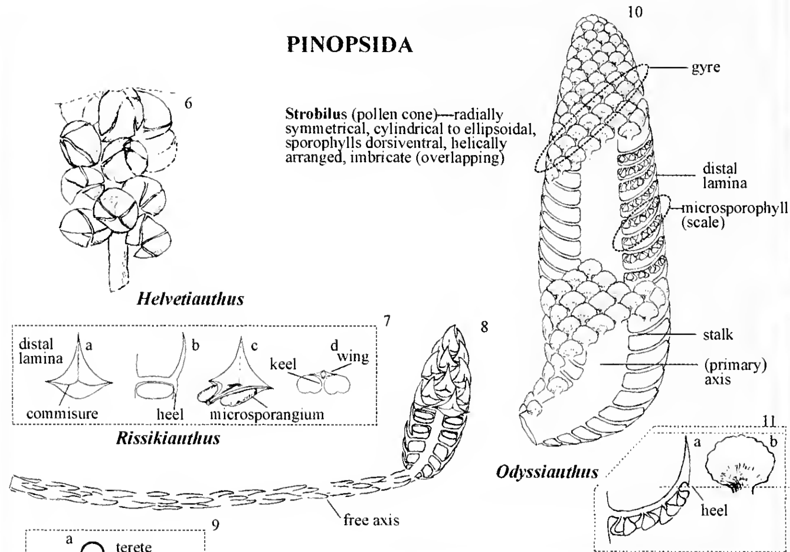
Microsporangium

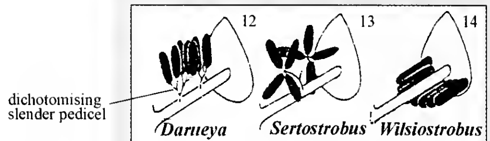
Pollen
small, oval, monosulcate (boat-shaped)

tfs 2–5 from Harris (1964), after Harris (1941), all *Androstrobus manis*, Gristhorpe Bed, Yorkshire Jurassic

PINOPSIDA

Strobilus (pollen cone)—radially symmetrical, cylindrical to ellipsoidal, sporophylls dorsiventral, helically arranged, imbricate (overlapping)

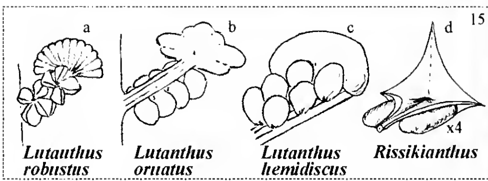




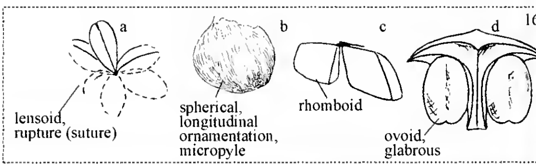
tfs 12–14 from Meyen (1987), after Grauvogel-Stamm (1978), Gres-a-Voltzia, France, Triassic

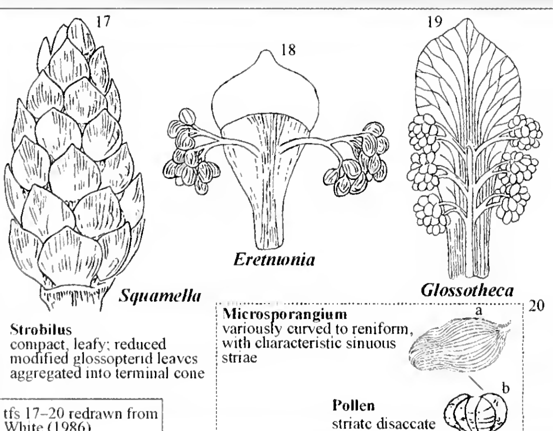
Microsporophyll
bilaterally symmetrical, simple scale, sporophyll stalk, terete (circular in transverse section, cylindrical and usually tapering), distal lamina, heel (keel), inner surface, external surface, peltate

episporangiate—adaxial
hyposporangiate—abaxial
perisporangiate—circum-axial
lateral
adaxial cluster
extant conifers: all pollen sacs develope on abaxial surface



Microsporangium (pollen sac)





Strobilus
compact, leafy; reduced modified glossopterid leaves aggregated into terminal cone

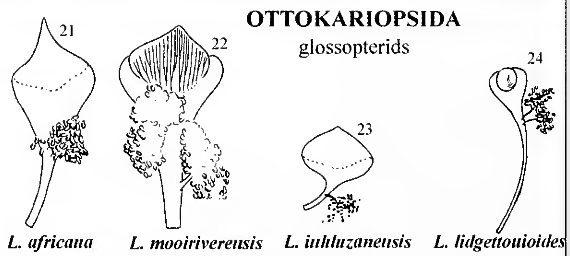
Microsporangium
variously curved to reniform, with characteristic sinuous striae

Pollen
striate disaccate

tfs 17–20 redrawn from White (1986), Gondwana Permian

OTTOKARIOPSIDA

glossopterids



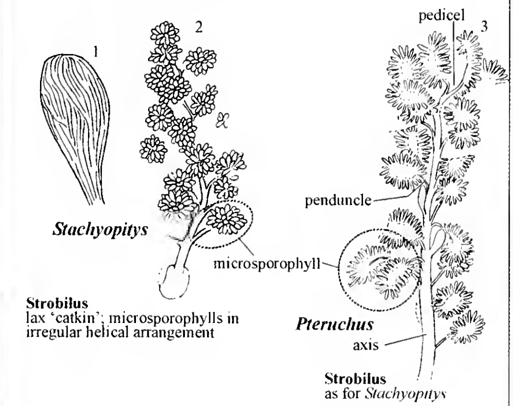
LIDGETTONIACEAE
Lidgettonia

Microsporophyll (fertiliger)
glossopterid scale-leaf, dense adaxial sporangial clusters, slender branching pedicel

tfs 21–24 from And. & And. (1985), Escourt Fm., South Africa, Late Permian

MORPHOLOGICAL TERMINOLOGY: male strobili

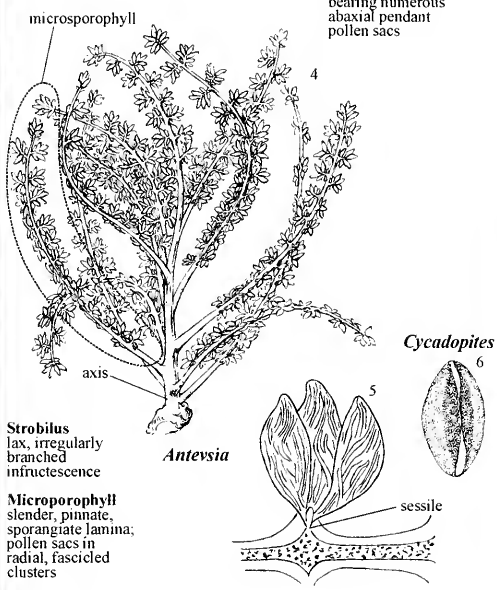
GINKGOOPSIDA



Strobilus
lax 'catkin'; microsporophylls in irregular helical arrangement

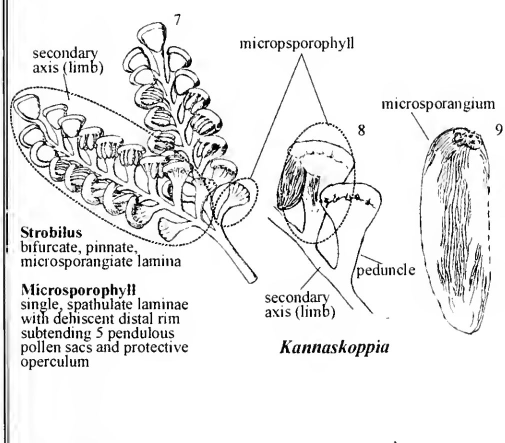
Strobilus
as for *Stachyopitys*

Microsporophyll
pedunculate, single or paired laminate heads bearing numerous abaxial pendant pollen sacs



Strobilus
lax, irregularly branched infructescence

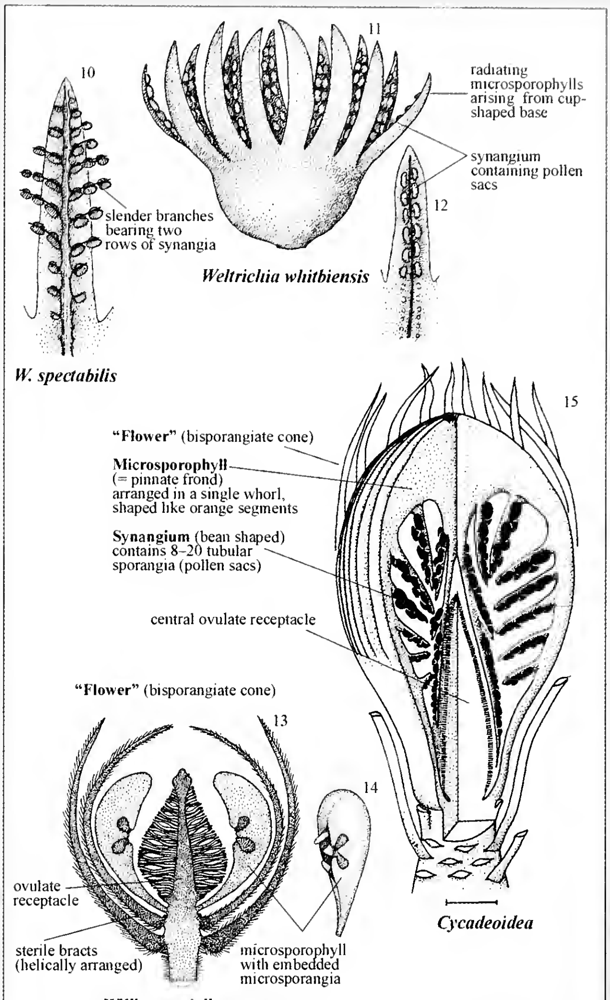
Microporophyll
slender, pinnate, sporangiate lamina; pollen sacs in radial, fascicled clusters



Strobilus
bifurcate, pinnate, microsporangiate lamina

Microsporophyll
single, spathulate laminae with dehiscent distal rim subtending 5 pendulous pollen sacs and protective operculum

BENNETTITOPSIDA

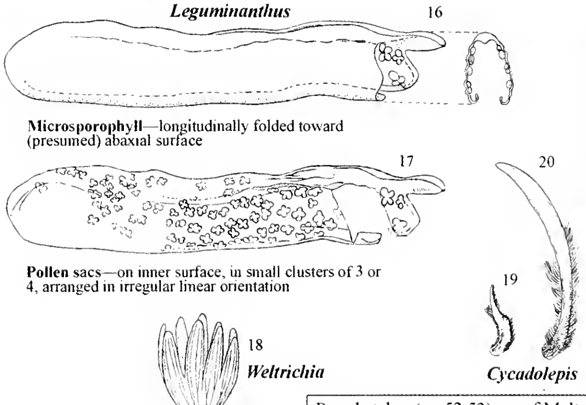


Williamsoniella coronata

monosporangiate cone (primitive condition) = dioecious
biosporangiate cone (derived) = monoecious

tfs 10–14 from Stewart & Rothwell (1993)
tf. 15 from Meyen (1987)
Euramerica,
Jurassic–Cretaceous

Leguminanthus



Microsporophyll—longitudinally folded toward (presumed) abaxial surface

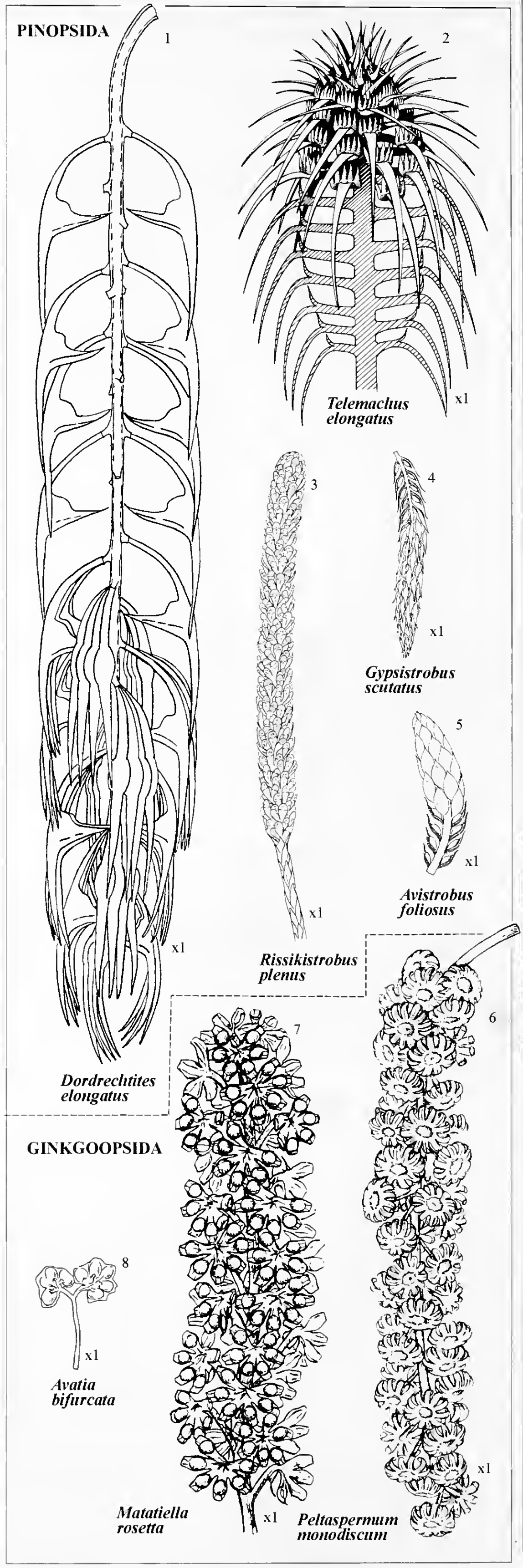
Pollen sacs—on inner surface, in small clusters of 3 or 4, arranged in irregular linear orientation

Pen sketches (pp 52,53) are of Molteno specimens unless otherwise indicated

Tab. 30. CLASSIFIED LIST OF MOLTENO GYMNOSPERMS

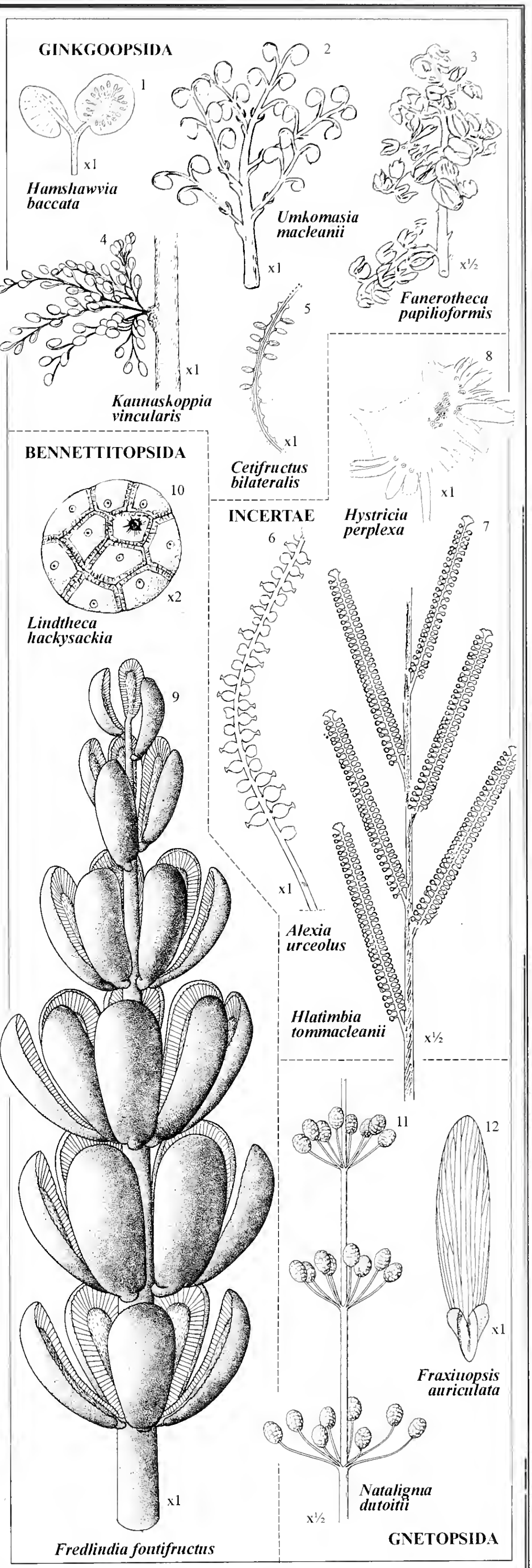
DIVISION
CLASS
ORDER
FAMILY
Genus & species

PINOPHYTA A.Cronquist, A.Takhtajan & W.Zimmermann 1966		
PINOPSIDA S.V.Meyen 1984		
DORDRECHTITALES order nov.		
DORDRECHTITACEAE fam. nov.		
Dordrechtites elongatus H.M.And. 1978	♀	60
" *cetiparvus* sp. nov.	-	-
" *mazocirrus* sp. nov.	-	-
VOLTZIALES order nov.		
FAMILIES INCERTAE SEDIS (2 families)		
Fredianthus maysiformis gen. et sp. nov.	♂	70
Lutanthus hemidiscus gen. et sp. nov.	♂	74
" *ornatus* gen. et sp. nov.	-	-
" *robustus* gen. et sp. nov.	-	-
VOLTZIACEAE R.Florin 1951		
Telemachus elongatus H.M.And. 1978	♀	82
" *grandis* sp. nov.	-	-
" *serribractus* sp. nov.	-	-
" *brachybractus* sp. nov.	-	-
" *dubibractus* sp. nov.	-	-
" *acutisquamus* sp. nov.	-	-
Odyssianthus crenulatus gen. et sp. nov.	♂	88
Heidiphyllum—1 foliage species	Ø	90
Clariphyllum—1 foliage species	Ø	100
PINALES S.V.Meyen 1984		
PODOCARPACEAE S.Endlicher 1847		
Rissikistrobus plenus gen. et sp. nov.	♀	102
" *semireductus* gen. et sp. nov.	-	-
" *reductus* gen. et sp. nov.	-	-
Rissikianthus concavus gen. et sp. nov.	♂	108
" *linearis* gen. et sp. nov.	-	-
" *townrowii* gen. et sp. nov.	-	-
" *convectus* gen. et sp. nov.	-	-
Rissikia—2 foliage species	Ø	112
FAMILY INCERTAE SEDIS		
Pagiophyllum—1 foliage species	Ø	124
ORDER INCERTAE SEDIS		
FAMILY INCERTAE SEDIS		
Gypsistrobus scutatus gen et sp. nov.	♀	126
Avistrobus foliosus gen. et sp. nov.	♀	130
ORDER INCERTAE SEDIS		
FAMILY INCERTAE SEDIS		
Helvetianthus tintinnabulum gen. et sp. nov.	♂	132
CYCADOPSIDA P.D.W.Barnard & A.G.Long 1975		
CYCADALES A.Engler 1892		
FAMILY INCERTAE SEDIS		
Androstrobus peninsiformis sp. nov.	♂	136
" *kraaiovalis* sp. nov.	-	-
Pseudoctenis—9 foliage species	Ø	140
FAMILIES INCERTAE SEDIS (3 families)		
Jeanjacquesia—3 foliage species	Ø	142
Ctenis—2 foliage species	Ø	144
Moltenia—4 foliage species	Ø	146
GINKGOOPSIDA S.V.Meyen 1984		
PELTASPERMALES S.V.Meyen 1984(?)		
PELTASPERMACEAE H.H.Thomas ex T.M.Harris 1937		
Peltaspermum thomasii T.M.Harris 1937	♀	148
" *monodiscum* sp. nov.	-	-
" *tridiscum* sp. nov.	-	-
" *turbanatum* sp. nov.	-	-
" *quindiscum* sp. nov.	-	-
Antevsia mazenodensis sp. nov.	♂	154
Lepidopteris—2 foliage species	Ø	156
Scytophyllum—1 foliage species	Ø	170
MATATIELLALES order nov.		
MATATIELLACEAE fam. nov.		
Matatiella rosetta gen. et sp. nov.	♀	172
" *hemirosetta* gen. et sp. nov.	-	-
" *sessilis* gen. et sp. nov.	-	-
" *reducta* gen. et sp. nov.	-	-
Kurtziana—16 foliage species	Ø	176
FAMILY INCERTAE SEDIS		
Switzianthus moriformis gen. et sp. nov.	♂	182
" *crispiformis* gen. et sp. nov.	-	-
Dejerseya—1 foliage species	Ø	186
GINKGOALES A.Engler 1897		
AVATIACEAE fam. nov.		
Avatia bifurcata gen. et sp. nov.	♀	192
Eosteria eosteranthus gen. et sp. nov.	♂	194
" *telemanthus* gen. et sp. nov.		-
Ginkgoites—6 foliage species	Ø	198
FAMILY INCERTAE SEDIS		
Paraginkgo—1 foliage species	Ø	208



Classified list

Taxon		Page
HAMSHAWVIALES order nov.		
HAMSHAWVIACEAE fam. nov.		
Hamshawvia baccata gen. et sp. nov.	♀	210
" *longipedunculata* gen. et sp. nov.	-	-
" *octosemina* gen. et sp. nov.	-	-
" *linisemina* gen. et sp. nov.	-	-
Stachyopitys matatilongus sp. nov.	♂	216
" *matatiramus* sp. nov.	-	-
" *gypsianthus* sp. nov.	-	-
" *lacrisporangia* sp. nov.	-	-
" *rotundisporangia* sp. nov.	-	-
" *maziramus* sp. nov.	-	-
Sphenobaiera—9 foliage species	*O*	222
UMKOMASIALES order nov.		
UMKOMASIACEAE S.V.Meyen 1984		
Umkomasia macleanii H.H.Thomas 1933	♀	240
" *bracteolata* sp. nov.	-	-
" *quadripartita* sp. nov.	-	-
" *decussata* sp. nov.	-	-
" *monopartita* sp. nov.	-	-
" *gracilliaxis* sp. nov.	-	-
" *capulata* sp. nov.	-	-
" *grandis* sp. nov.	-	-
Pteruchus africanus H.H.Thomas 1933	♂	250
" *matatimajor* sp. nov.	-	-
" *helvetigracilis* sp. nov.	-	-
Dicroidium—19 foliage species	*O*	256
Fanerotheca papilioformis sp. nov.	♀	272
" *waldeckiformis* sp. nov.	-	-
" *cruciformis* sp. nov.	-	-
" *elandiformis* sp. nov.	-	-
PETRIELLALES T.N.Taylor *et al.* 1994		
KANNASKOPPIACEAE fam. nov.		
Kannaskoppia vincularis gen. et sp. nov.	♀	286
Kannaskoppianthus lutinumerus gen. et sp. nov.	♂	290
" *matatiparvus* gen. et sp. nov.	-	-
" *irregularis* gen. et sp. nov.	-	-
" *telemagnus* gen. et sp. nov.	-	-
Kannaskoppifolia—10 foliage species	*O*	294
ORDER INCERTAE SEDIS		
FAMILY INCERTAE SEDIS		
Cetifructus bilateralis gen. et sp. nov.	♀	314
CLASS INCERTAE SEDIS		
ALEXIALES order nov.		
ALEXIACEAE fam. nov.		
Alexia urceolus gen. et sp. nov.	♀	318
CLASS INCERTAE SEDIS		
HLATIMBIALES order nov.		
HLATIMBIACEAE fam. nov.		
Hlatimbia tommacleanii gen. et sp. nov.	♀	322
Batiopteris—5 foliage species	*O*	324
CLASS INCERTAE SEDIS		
ORDER INCERTAE SEDIS		
FAMILY INCERTAE SEDIS		
Hystricia perplexa gen. sp. nov.	♀	330
CLASS INCERTAE SEDIS		
ORDER INCERTAE SEDIS		
FAMILY INCERTAE SEDIS		
Saportaea—1 foliage species	*O*	332
CLASS INCERTAE SEDIS		
ORDER INCERTAE SEDIS		
FAMILY INCERTAE SEDIS		
Linguifolium—1 foliage species	*O*	334
BENNETTITOPSIDA		
FREDLINDIALES order nov.		
FREDLINDIACEAE fam. nov.		
Fredlindia fontifructus gen. et sp. nov.	♀	336
Weltrichia regalis sp. nov.	♂	340
" *helvetirara* sp. nov.	-	-
Cycadolepis rexiplumea sp. nov.	♂	341
Leguminanthus leopardus sp. nov.	♂	342
Halleyoctenis—3 foliage species	*O*	344
PENTOXYLALES R.K.E.Pilger & H.Melchior 1954		
LINDTHECACEAE fam. nov.		
Lindtheca hackysackia gen. et sp. nov.	♀	356
Taeniopteris—8 foliage species	*O*	358
GNETOPSIDA H.G.A.Engler 1854		
NATALIGMALES order nov.		
NATALIGMACEAE fam. nov.		
Nataligma dutoitii gen. et sp. nov.	♀	362
Gontriglossa—1 foliage species	*O*	364
ORDER INCERTAE SEDIS		
FAMILIES INCERTAE SEDIS (2 families)		
Graciliglossa—1 foliage species	*O*	368
Cetiglossa—1 foliage species	*O*	369
FRAXINOPSIALES order nov.		
FRAXINOPSIACEAE fam. nov.		
Fraxinopsis andium (J.Frenguelli 1941) comb. nov.	♀	370
" *auriculata* sp. nov.	-	-
" *cornicordis* sp. nov.	-	-
Yabeiella—2 foliage species	*O*	376
Jungites—2 foliage species	*O*	384



6. ON THE PHYLOGENY OF THE PINOPSIDA

With particular reference to the male cone genera and, more specifically, those from the Molteno.

State of knowledge

The phylogeny and classification of the genera of fossil coniferopsids remain largely unresolved. Recent general texts reflect considerable differences in viewpoint (Meyen 1987; Stewart & Rothwell 1993; Taylor & Taylor 1993). We adopt the order Voltziales in the sense of Stewart & Rothwell (1993) as a group 'transitional' between the Cordaitales and Coniferales, and the Voltziaceae as a group intermediate between the Utrechtiaceae and modern conifers. In particular we conceive the family Voltziaceae as detailed in And. & And. (1989).

Male coniferous cones, aside from those found in the Molteno, are entirely unknown in collections from elsewhere around the Gondwana Triassic. Similar levels of infrequency (productive sites) and rarity (individuals per site) appear to be the pattern throughout the fossil record globally. They have added very little to our fragmentary knowledge of the phylogeny of the Pinopsida.

While the Molteno cones contribute substantially to the sum total material available for study, they do not help clarify the lineages and relationships within the group. What they do suggest is that pinopsid evolution during the Triassic may have been a good deal more complex than reflected in Tab. 31 opposite.

Ottokariopsida (glossopterids)

As reflected in And. & And. (1985, pp. 106–145) and widespread elsewhere in the literature, the Ottokariopsida and Cordaitanthales—apparent stem group to all later pinopsids—have much in common. Their relationship is certainly not resolved: did they share some common ancestor, did the ottokariopsids arise from the Cordaitanthales, should they be grouped more closely than shown here? We do not aim to explore these possibilities further beyond commenting on the enigmatic options suggested by the male conifer cones of the Molteno.

Did the southern conifers, or some clades thereof, evolve from the glossopterids as suggested by White (1986, pp. 122–125)? *Fredianthus*, *Lutanthus* and *Odyssianthus*, the Molteno male cones placed here within the Voltziales, show certain features unlike those in the Laurasian Carboniferous to Triassic voltzialean cones, yet shared by the glossopterid family Lidgettoniaceae (And. & And. 1985, pp. 133–136; White 1986, pp. 118–121). These glossopterid features, appearing variously in the Molteno cones, include the double row of microsporangia and the generally leafy aspect to the scales—with most species characterised by distinct wings (astride a midrib) along the scale axis and by the absence of a heel to the distal lamina (i.e. being nonpeltate).

Cordaitanthales

Lea Grauvogel-Stamm (pers. comm., Pretoria, 15.11.1999) feels that *Fredianthus* can be compared to the genus *Cladostrobus* (Maheshwari & Meyen 1975; Meyen 1987), a cone associated with the leaf *Rufloria* and found widespread in the Upper Permian of Siberia and Mongolia (see tf. 25, p. 59). *Cladostrobus* is a far smaller cone (over 60 mm long and *ca* 15 mm in diameter). The microsporophylls, consisting of a gracile terete stalk and rhomboid distal lamina, bear groups of up to eight (oval to oval-elliptical) microsporangia. Neither the degree of clustering, if any, nor the nature of the attachment of the pollen sacs, however, is clear. Meyen (1987) reconstructs and describes the microsporophylls as perisporangiate (sacs all around the stalk) rather than hyposporangiate (adaxial), with no suggestion of clustering.

It is possible that *Fredianthus*, in the Molteno, represents a distinct, surviving cordaitanthalean lineage rather than falling in the mainstream of the Voltziales. Short of further information, we follow the voltzialean option.

Voltziales

Voltziaceaen foliage and female cones are very characteristic components of global floras from the Upper Permian to Middle Jurassic (And. & And. 1989, pp. 420–423), yet the male cones barely make an appearance. As far as we are aware, the only previously described polleniferous cones reasonably established as belonging to the family are the group of genera *Sertostrobus, Darneya* and *Willsiostrobus* deriving from the lower Middle Triassic *Voltzia* Sandstone and approximate time equivalents elsewhere in Europe and beyond in Laurasia (Grauvogel-Stamm 1978; Taylor 1988; Grauvogel-Stamm & Galtier 1998). Well preserved *Willsiostrobus* specimens have also been described from late Lower Triassic beds in N. China (Wang & Wang 1990). A further record is that of Krassilov (1982): *D. angusta* and *W. latisaccus* from the Lower Cretaceous of Mongolia.

The three genera of putative voltzialean male cones, *Fredianthus*, *Lutanthus* and *Odyssianthus*, described here from the Molteno, add, as previously noted, significantly to the spectrum of taxa and morphology at hand.

Although largely distinct from the European voltziaceaen male cones, the three Molteno forms are all included provisionally in the order Voltziales: *Fredianthus* and *Lutanthus*, without any foliage or megasporangiate affiliates, in two unspecified families; *Odyssianthus*, with well-established foliage (*Heidiphyllum*) and female-cone (*Telemachus*) affiliates, in the Voltziaceae. Both *Heidiphyllum* and *Telemachus* are undisputed members of the family Voltiaceae as currently constituted.

Odyssianthus with its two rows of latero-abaxial, clustered, sessile pollen sacs, *Fredianthus* with its single row of abaxial, clustered, near-sessile sacs, and *Lutanthus* covering a wide spread of morphological types, hint at family- and order-level diversity in the Late Triassic pinopsids markedly richer than reflected in our present classification based on ovulate material alone.

The *Voltzia* Sandstone genera likewise show considerable differences from one another, suggesting, already in the early Middle Triassic, a diversity amongst the nonpinalean pinopsids not yet fully recognised. While *Darneya* and *Sertostrobus* bear adaxial sporangia along the stalk, *Willsiostrobus* sports pollen sacs that are abaxially attached to the heel of the distal lamina. Grauvogel-Stamm & Galtier (1998), moreover, interpret *Darneya* as bearing a complex microsporophyll—with fused scale and bract—and propose the presence of two strongly divergent lineages of conifer in their material. Perhaps the three French genera represent three major lineages, only one of which is voltzialean.

Aside from the Molteno material, male cones of the order remain unknown from the Gondwana Triassic—although *Heidiphyllum* foliage is very widespread and often a dominant component of assemblages.

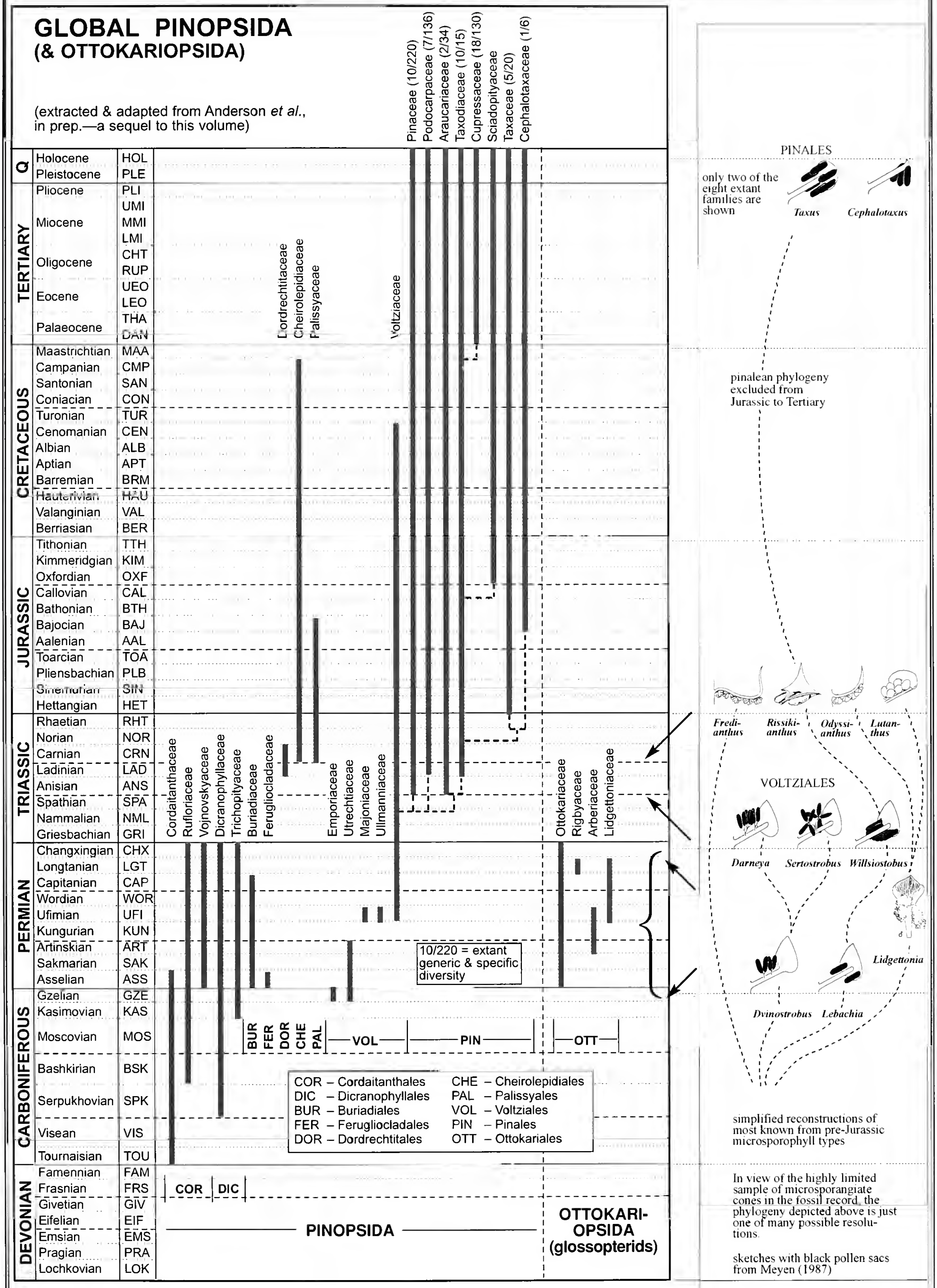
Pinales

Both *Lebachia*, included in the Utrechtiaceae (Lebachiaceae, Walchiaceae), and *Willsiostrobus* (Middle Triassic, Europe) in the Voltziaceae, show horizontally alligned microsporangia attached to the distal lamina of a strongly peltate scale. These are features almost ubiquitously characterising the Pinales, the diverse crown group of Pinopsida. *Rissikianthus*, from the Molteno, likewise shares these features. Did such characters arise independently several times within the stem Pinopsida; is some definite reshuffling of taxa within the Carboniferous to Triassic families indicated; are the families quite wrongly conceived at present? The reality of pinopsid phylogeny is as yet elusive. A quantum jump in the available sample of male cones will, no doubt, contribute to the resolution sought.

Primitive & derived characters

If it is true, as generally supposed, that the Cordaitales are the stem group leading to all later pinopsids (and possibly the ottokariopsids), then it is amongst this group back in the Early to Middle Carboniferous that we must seek their primitive characters. Unfortunately male cones of this critical vintage and order appear unknown. We move then directly to the Voltziales and Ottokariales of the latest Carboniferous and Permian (see Tab. 31).

At least three markedly different kinds of cone already existed: in *Dvinostrobus*, *Lebachia* and *Lidgettonia*. They differ in virtually every diagnostic feature characterising male cones of these late Palaeozoic orders. With this morphological spectrum as a starting point, all features defining these genera are witnessed as equally primitive and all features newly evident in Mesozoic pinopsid males as derived.



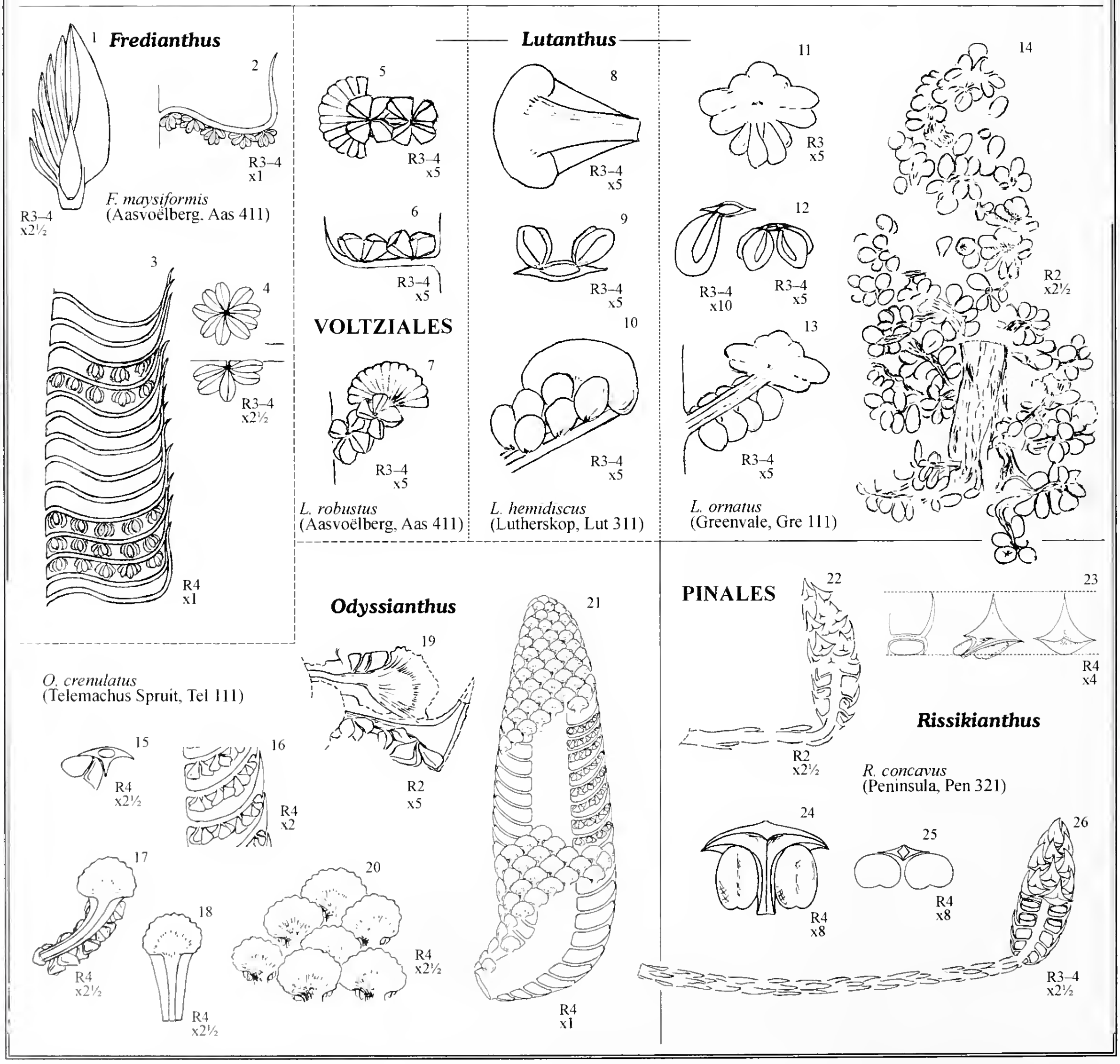
Tab. 31. Time range & phylogeny of Pinopsida & Ottokariopsida

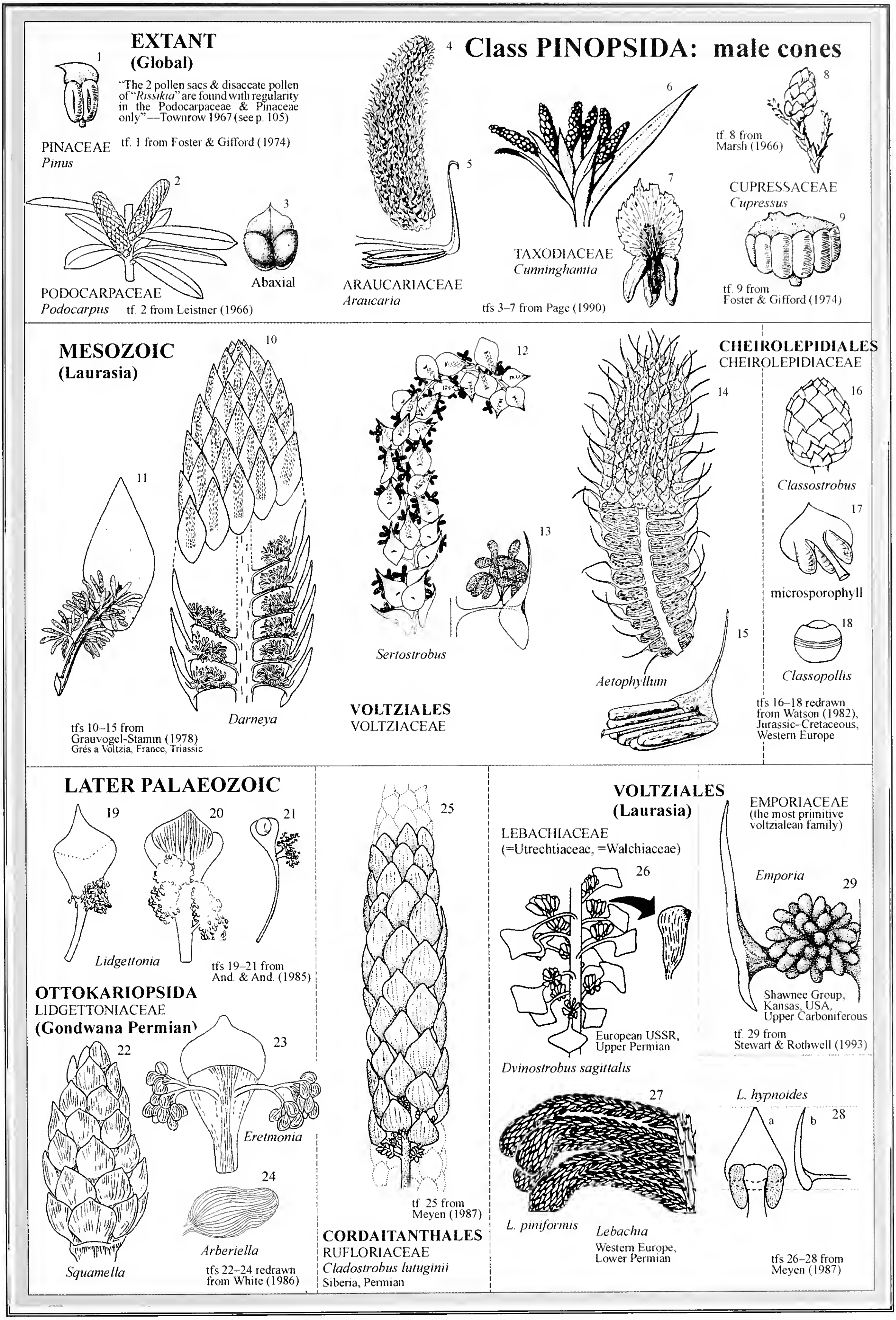
MOLTENO PINOPSIDA: male cones

Tab. 32. Diagnostic features of the four voltzialean & pinalean genera

	Voltziales			Pinales
	Fredianthus	*Luthanthus*	*Odyssianthus*	*Rissikianthus*
Strobilus				
Size	to 220 mm in length	30–40 mm in length	70 mm in length	10–18 mm in length
Gyres	60 of 25–30 microsporophylls	13–24 of 10–20 microsporophylls	23 of 16–20 microsporophylls	7–10 of 6–12 microsporophylls
Axis	moderately flexed	strongly flexed to erect	strongly flexed to base	strongly flexed to base
Microsporophyll				
Stalk	sigmoidal	curving upward distally	strongly upward-curving	straight
Lamina	narrowly ovate, leafy multilobed/dentate, without heel	broad, leafy entire to multi-ribbed, without heel	broadly ovate, leafy finely crenulated, with moderate heel	triangular, woody entire, with strong heel
Microsporangia	single median row, 5 clusters along the row, 45 sacs per scale, abaxial (along stalk)	1 median or 2 lateral rows, 3–4 singles or 2 clusters, 6–8 sacs per scale, adaxial to abaxial (along stalk)	in 2 lateral rows, 4 clusters per row, 22–24 sacs per scale, latero-abaxial (along stalk)	a single pair, 1 single per side, 2 sacs per scale, abaxial (from heel)
Microsporangium				
Shape	elliptical	obovate to rhomboidal	irregularly rhomboidal	rotund
Dehiscence	clear longitudinal line	usually with clear longitudinal line & apical "micropyle"	clear longitudinal line & apical "micropyle"	longitudinally bilobed (no obvious dehiscence)

All numbers (with a few exceptions) are approximate





EXTANT
(Global)
"The 2 pollen sacs & disaccate pollen of "Rissikia" are found with regularity in the Podocarpaceae & Pinaceae only"—Townrow 1967 (see p. 105)
PINACEAE
Pinus
tf. 1 from Foster & Gifford (1974)
Class PINOPSIDA: male cones
PODOCARPACEAE
Podocarpus
tf. 2 from Leistner (1966)
Abaxial
ARAUCARIACEAE
Araucaria
TAXODIACEAE
Cunninghamia
tfs 3–7 from Page (1990)
tf. 8 from Marsh (1966)
CUPRESSACEAE
Cupressus
tf. 9 from Foster & Gifford (1974)
MESOZOIC
(Laurasia)
Darneya
tfs 10–15 from Grauvogel-Stamm (1978)
Grès a Voltzia, France, Triassic
Sertostrobus
VOLTZIALES
VOLTZIACEAE
Aetophyllum
CHEIROLEPIDIALES
CHEIROLEPIDIACEAE
Classostrobus
microsporophyll
Classopollis
tfs 16–18 redrawn from Watson (1982), Jurassic–Cretaceous, Western Europe
LATER PALAEOZOIC
Lidgettonia
tfs 19–21 from And. & And. (1985)
OTTOKARIOPSIDA
LIDGETTONIACEAE
(Gondwana Permian)
Squamella
Eretmonia
Arberiella
tfs 22–24 redrawn from White (1986)
tf. 25 from Meyen (1987)
CORDAITANTHALES
RUFLORIACEAE
Cladostrobus lutuginii
Siberia, Permian
VOLTZIALES
(Laurasia)
LEBACHIACEAE
(=Utrechtiaceae, =Walchiaceae)
European USSR, Upper Permian
Dvinostrobus sagittalis
EMPORIACEAE
(the most primitive voltzialean family)
Emporia
Shawnee Group, Kansas, USA, Upper Carboniferous
tf. 29 from Stewart & Rothwell (1993)
L. hypnoides
L. piniformis
Lebachia
Western Europe, Lower Permian
tfs 26–28 from Meyen (1987)

PINOPSIDA S.V.Meyen 1984
DORDRECHTITALES J.M.And. & H.M.And., ord. nov.
DORDRECHTITACEAE J.M.And. & H.M.And., fam. nov.

Dordrechtites H.M.And. 1978

Type species
Dordrechtites elongatus H.M.And. 1978.

Generic diagnosis
A pinopsid female cone bearing fascicles of gracile, T-shaped, ovulate scales that detach readily from short stout pedicels.

Generic characters
Attachment: unknown.
Strobilus: simple, compact to lax cone, broadly linear, medium to large (to *ca* 150 x 22 mm); axis slender, curved, pendent; scale clusters subopposite, subdecussate.
Megasporophyll: in fascicles of 3 or 4 parallel to partly overlapping ovuliferous scales, readily detaching from short stout pedicels.
Ovuliferous scale: T-shaped (30 x 10 mm); sterile arms of T roughly equal, gracile, linear, dorsiventrally flattened; proximal arm strongly arcuate, tapering to square apex at attachment; distal arm mildly arcuate, tapering to finely acute tip; ovuliferous trunk of T relatively short, robust, triangular in side view, curving proximally, dorsiventrally flattened, broadly ovate to obovate in plan view, with strong ventral keel, broad lateral laminar wings and mucronate tip.
Ovule/seed: adaxial, enclosed dorsally within winged ovuliferous trunk and never found detached, narrowly ovate in plan, dorsiventral.
Cuticular features: see text below.

Etymology
Dordrechtites—after the town Dordrecht situated near the type locality.

Global range: 4 spp., Gondwana, Tr. (LAD–CRN).
First: *Dordrechtites* sp. (Holmes, pers. comm.); Dubbo district, N.S.W., Australia.
Last: *Dordrechtites* sp. (HMA, this vol., p. 61); Aqua de la Pena, Ischigualasto, Argentina.

Gondwana Triassic occurrence
SAm—N. Argentina, 1 loc. (>6 indivs).
SAf—Karoo Basin, 18 TCs (>413 indivs).
Aus—Queensland and New South Wales, 2 locs (>120 indivs).

Molteno occurrence
Frequency (F): 17 TCs (of 100 sampled in Molteno).
Diversity (D): 3 species.
Abundance (A): 413 individuals, common to very rare.

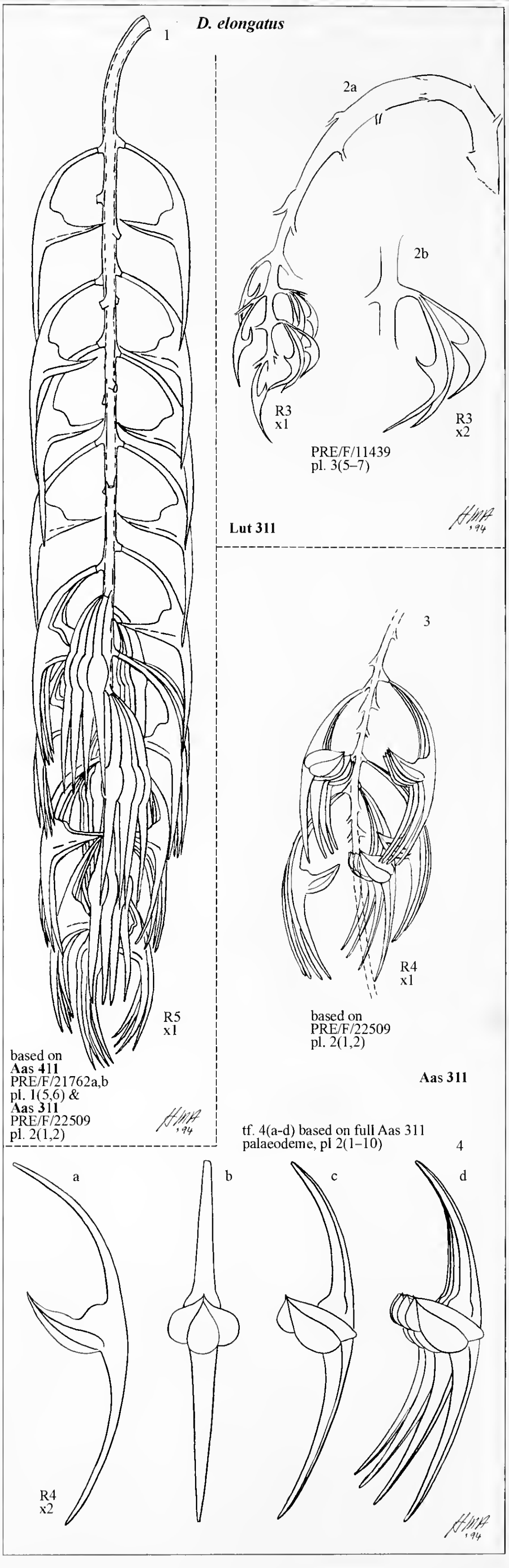
Lut 311 Hei elo:	>50	indivs in	50	man-hrs cleaving	(common)
Aas 411 Dic/Sph:	>100	" "	512	" "	(occasional)
Aas 311 Hei elo:	>40	" "	140	" "	(occasional)
Bir 111 Sph 2spp:	>50	" "	550	" "	(occasional)
Maz 211 Hei/Dic:	40	" "	85	" "	(5 per 1 man-day) rare
Lit 111 Dic/Hei:	>50	" "	550	" "	(>1 per 1 man-day) rare
Umk 111 Dic 2spp:	10	" "	400	" "	(1 per 4 man-days) very rare

Whereas intact or partially intact cones of *Dordrechtites* are extremely to vanishingly rare, the dehisced ovuliferous scales are, in a good many TCs and especially on certain bedding planes, occasional to common.

Affiliated organs
Male cone: unknown.
Foliage: unknown (but see p. 62).

Classification & comparison
Suprageneric classification (Dordrechtitaceae/Dordrechtitales)
The cones and ovuliferous scales of *Dordrechtites* offer a pinopsid impression, but the extraordinary mode of attachment of the scales in pedicellate fascicles is unique (either as reconstructed here, or as interpreted in Playford *et al.* 1982, for the Australian species—see p. 63). While it would stretch comparisons unduly to consider *Dordrechtites* as falling either within the Voltziales or the Pinales, it seems reasonable to include the genus in the class Pinopsida as a new family (Dordrechtitaceae) and order (Dordrechtitales). The Voltziales represent the most likely known sister clade.

Intergeneric comparison (Gondwana Triassic)
Nothing comparable is known.



Reconstructions

The set of Grade 3–5 reconstructions (p. 60, tfs 1–4) of the type species, *D. elongatus*, is based largely on the selection of specimens (Grade 2 reconstructions, p. 64 [1–10]) from the reference palaeodeme and top three sister palaeodemes—Aas 411, Bir 111, Aas 311 and Lut 311—for the species. In view of the morphological uniqueness of this genus, we elaborate more fully than usual on the relative certainty of the reconstructions.

Mature cone (p. 60, tfs 1, 3)

The mature strobilus is fairly confidently portrayed as terminal, pendulous and occurring singly at the end of arching branchlets. Its length is based on the most substantial specimen from Aas 411 (PRE/F/21762 a,b; p. 64, tf. 3), backed up by a bare axis of *ca* 150 mm from the Moolayember Fm. of Australia (Playford *et al.* 1982, pl. 2, fig. 4), with the base apparently preserved, but the apex missing. The pendulous nature is deduced from the gracile, generally curving axis and the strongly curved proximal end in the single available immature specimen (Lut 311, PRE/F/11439, p. 60, tf. 2a,b). The subopposite, subdecussate attachment of the scale clusters is based on PRE/F/21762 a,b (p. 64, tf. 3) from Aas 411 and PRE/F/22509 (p. 64, tf. 4) from Aas 311.

Immature cone (p. 60, tf. 2a,b)

The single, partly intact cone from Lut 311 (PRE/F/11439; p. 64, tf. 9) bears scales less than half normal size. The specimen could represent a distinct species, but since all further single or clustered scales from Lut 311 (p. 64, tfs 8, 10) are like those of *D. elongatus* from other TCs in size and form, it is assumed to be an immature cone.

Ovuliferous scales (p. 60, tfs 4a–d)

The number of scales in the scale clusters on a mature intact cone remains uncertain. Nowhere in the few partly intact cones at hand (p. 64, tfs 2–4, 9, 10) is the number sure. It is evident that in the closed cone the arms of the scales lie immediately adjacent to one another, while the winged ovules overlap strongly. We favour clusters of four scales (only slightly over three) as the norm and have drawn the reconstructions on this basis.

Ovule & seed

While the great majority of dehisced scales are preserved in lateral view, they are very occasionally seen straight on with the ovule in full or partial dorsiventral aspect (p. 64, tfs 5–7, 10) allowing the interpretation as shown. The ovuliferous part of the scale is clearly dorsiventrally flattened and is markedly winged. In only one specimen (Aas 311; PRE/F/22515; p. 64, tf. 6) is the intact seed preserved.

Classification (elaborated)

Laurasia Triassic

The closest apparent comparison amongst Voltzialean genera is with *Borysthenia* of Russia, Donets Basin, Upper Triassic (Stanislavsky 1976, p. 77–81, pl. 43–47; And. & And. 1989, p. 423). Aside from the scales, *Dordrechtites* is distinct in having clear pedicels from which the scale fascicles detach.

Other ages

The seed of the extant *Araucaria* (Coniferales) is superficially similar to the central winged seed/ovule of *Dordrechtites*—which is, however, invariably found with the two linear projections.

Some similarity occurs with the winged seed *Semenalatum paucum* (Dilcher *et al.* 1997) from the Early Permian of China and thought by them to have coniferous affinities. This seed, however, is characterised by two lateral wings and one limited median projection, and the point of attachment is central where three additional, short, sterile scales occur.

In other plant divisions we have encountered two fossils that bear a remote resemblance to the *Dordrechtites* scale. Douglas (1969) describes an isolated angiosperm seed, *Lappacarpus*, with two appendages, but these are very thin and only 2–5 mm long. Within the Lycophyta, *Cantheliophorus* (Thomas & Brack-Hanes 1991) shows only a single extension, but this is clearly leaf-like with a single midrib.

Gondwana Triassic occurrence (elaborated)

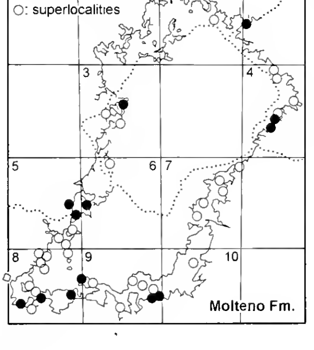
Dordrechtites, frequent and abundant in the Molteno—at least as dehisced scales—remains very sparsely known elsewhere in the Gondwana Triassic. Only three TCs yielding the genus are known outside of Africa.

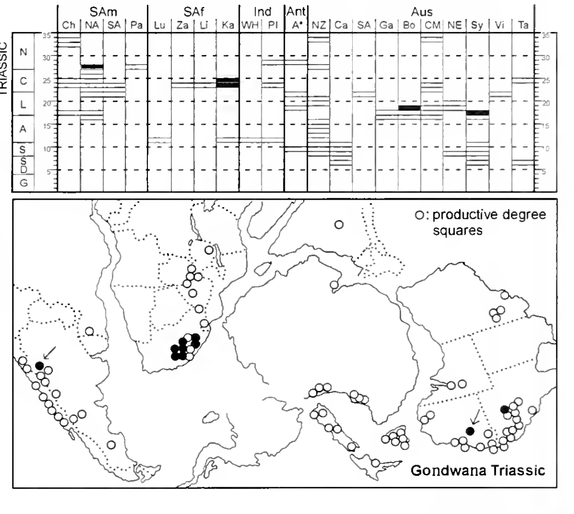
South America

Definite *Dordrechtites* scales with *Heidiphyllum* leaves were recorded on a bedding plane by HMA (unpublished notes, 23-09-1999) at Agua de la Pena locality (Los Rastros Fm.) during the VII International Symposium on Mesozoic Terrestrial Ecosystems field excursion to Ischigualasto, Argentina. No material was collected.

Australia

A well-represented *Dordrechtites* palaeodeme, including two broken cones (one being indistinctly preserved) and over 120 isolated scales, is known from a single 'locality' in the Lower Ladinian Moolayember Fm., Bowen Basin, Queensland (Playford *et al.* 1982; for further details see pp. 62, 63). This remains the only published occurrence of the genus outside the Molteno. Keith Holmes (pers. comm.) has seen rare isolated scales at a locality in the Dubbo district, New South Wales.





assemblages (taphocoenosis)		*Heidiphyllum*	♀ *Telemachus*	♀ *Dordrechtites*	*Dordrechtites* intactness				man-hours cleaving
					1–2 scales	3–10 scales (clusters)	>10 scales (clusters)	scales attached	
Nav 111	Dic odo	1	-	-	-	-	-	-	2
Cal 211	Hei elo	75	-	-	-	-	-	-	2
Bir 211	Sph 2spp	3	-	-	-	-	-	-	7
" 311	Hei/Sph	45	-	6	6	-	-	-	2
" 111	Sph 2spp	10	-	50	47	2	1	-	550
Dor 111	Hei elo	85	-	-	-	-	-	-	2
Gre 121	Hei elo	98	100	-	-	-	-	-	10
" 111	Sph pon	10	-	-	-	-	-	-	5
Boe 111	Lep sto	7	-	-	-	-	-	-	8
" "	Dic/Hei	42	-	-	-	-	-	-	8
" 112	Dic cor	14	-	2	2	-	-	-	6
Cyp 111	Dic cra	24	5	-	-	-	-	-	100
" 111	Hei elo	100	-	-	-	-	-	-	2
Kan 112	Hei elo	98	10	-	-	-	-	-	15
" 111	Ast spA	10	-	-	-	-	-	-	30
Tel 111	Hei elo	89	40	-	-	-	-	-	90
Vin 111	Dic odo	28	-	-	-	-	-	-	10
Ela 111	Dic oco	7	1	-	-	-	-	-	10
Kra 311	Dic odo	5	-	-	-	-	-	-	13
Lut 111	Hei/Dic	50	2	-	-	-	-	-	2
" 511	Hei elo	80	1	-	-	-	-	-	2
" 411	Hei/Dic	50	12	-	-	-	-	-	2
" 311	Hei elo	99	-	50	47	1	1	1	50
Tin 121	Sph 2spp	4	-	-	-	-	-	-	5
" 111	Sch sp	10	-	-	-	-	-	-	3
" 131	Hei/Ast	50	-	-	-	-	-	-	3
Kon 223	Dic odo	1	-	-	-	-	-	-	7
" 211	Hei elo	95	-	-	-	-	-	-	1
" 111	Dic odo	7	-	1	1	-	-	-	34
" "	Equ sp	10	-	-	-	-	-	-	1
" "	Hei elo	84	2	18	9	5	4	-	4
Pen 321	Dic/Ris	1	1	-	-	-	-	-	35
" 211	Dic/Equ	2	-	-	-	-	-	-	4
" 421	Dic odo	4	-	-	-	-	-	-	7
" 431	Dic/Equ	5	-	-	-	-	-	-	1
" 311	Hei elo	75	17	5	5	-	-	-	35
" 411	" "	94	50	1	1	-	-	-	70
Kle 111	Neo car	1	-	-	-	-	-	-	4
" "	Hei elo	90	25	-	-	-	-	-	15
" "	Hei/Dic	49	-	-	-	-	-	-	9
Kap 111	Dic/Ris	25	5	-	-	-	-	-	65
Ela 112	Dic/Hei	30	-	-	-	-	-	-	4
Nuw 211	Dic 2spp	1	-	4	4	-	-	-	6
Win 111	Hei elo	79	-	15	6	3	6	-	20
Qua 111	Dic odo	20	-	-	-	-	-	-	8
Maz 111	Dic cra	5	-	-	-	-	-	-	30
" 211	Hei/Dic	32	-	40	38	2	-	-	85
Hla 213	Dic elo	1	-	-	-	-	-	-	60
Umk 111	Dic 2spp	7	-	10	10	-	-	-	400
Inj 211	Dic dub	10	-	-	-	-	-	-	2
San 111	Dic cra	5	-	15	15	-	-	-	30
Mng 111	Dic 2spp	6	-	-	-	-	-	-	2
Qac 111	Hei/Dic	50	10	-	-	-	-	-	4
Mat 111	Dic dub	4	12	-	-	-	-	-	65
Lit 111	Dic/Hei	23	-	50	46	4	-	-	550
Aas 611	Hei elo	80	6	-	-	-	-	-	3
" 111	" "	77	12	-	-	-	-	-	40
" 211	" "	100	-	6	6	-	-	-	35
" 311	" "	99	-	40	37	1	1	1	140
" 411	Dic/Sph	1	-	100	67	15	15	3	512
" 511	Dic elo	20	-	-	-	-	-	-	2
Bam 111	Dic dub	1	-	-	-	-	-	-	3
Total TCs		62	18	17	17	8	6	3	
Total indivs		%	311	413	347	33	28	5	

Tab. 33. *Dordrechtites*, Molteno occurrence

Abundance: *Dordrechtites* may be quite abundant at certain TCs and it is possible to collect numerous individuals. In these cases, we record the number of individuals (rounded off where *ca* 40 indivs or above) as curated for the genus, but do not include further specimens which occur on slabs in the remainder of the collection.

Evidence for affiliation of organs

Dordrechtites & Telemachus (mutually exclusive genera)

The distribution pattern of the two ovulate organs, *Dordrechtites* and *Telemachus*, in the 100 Molteno assemblages is an intriguing one (Tab. 33). *Dordrechtites*, a cone scale of still uncertain affinity, is known from 17 assemblages; *Telemachus*, the voltzialean coniferous cone affiliating with the abundant leaf *Heidiphyllum*, is known from 18 assemblages. Both genera are invariably found in beds yielding *Heidiphyllum*—known from 62 assemblages, often as the monodominant element—but their occurrence is virtually mutually exclusive. What does this striking pattern suggest with regard to depositional environment, taphonomy and affiliation?

On Heidiphyllum (two foliage genera or one?)

An option that has been entertained is that the genus *Heidiphyllum* actually includes two quite distinct, though superficially similar, foliage genera. [We have previously, in our study of the Molteno flora, separated out *Sphenobaiera insecta* from Umk 111 (And. & And. 1989, p. 144). The taxon looks very like *Heidiphyllum* in shape, size and venation, but is undoubtedly a species of *Sphenobaiera* based on cuticle and the finer details of venation.] After close examination of a good number of *Heidiphyllum* palaeodemes from TCs including either *Dordrechtites* or *Telemachus*, we found no sign of two foliage genera. A very characteristic feature of *Heidiphyllum*, allowing its sure identification, is the clear presence of interveinal striae (And. & And. 1989, pls 249–263). This occurs in all palaeodemes examined.

Dordrechtites as a pinopsid (the taphonomic filter)

If *Dordrechtites* is correctly classified as representing a new order in the class Pinopsida, we might expect the foliage of the plant to appear typically coniferalean. In view of the frequent and abundant occurrence of *Dordrechtites* in Molteno strata one would also imagine the parent plant to be a prominent element characterising certain communities in the Molteno Biome. How is it that the foliage could have been totally filtered out in the taphonomic/fossilisation process? The question remains unresolved.

The pinopsid-foliage enigma does not end with *Dordrechtites*. We have identified five pinopsid male-cone genera in the Molteno, for three of which, *Fredianthus*, *Lutanthus* and *Helvetianthus*, there occur no evident foliage affiliates (Tab. 34, p. 75). And we recognise five female-cone genera (only two with male-cone affiliates), three of which, *Dordrechtites*, *Gypsistrobus* and *Avistrobus*, likewise have no evident foliage affiliates. These other fruit genera, unlike *Dordrechtites*, are all extremely infrequent and rare. Overall, then, there occur six pinopsid whole-plant genera represented by male or female cones, but whose foliage, apparently, has been comprehensively filtered through the taphonomic net.

The particular difficulty in establishing affiliations between dispersed pinopsid organs in a well-sampled formation is not unique to the Molteno. The *Voltzia* Sandstones of the French Lower Triassic yield a rich pinopsid-dominated flora with several distinctive female, male and foliage genera. After careful curation, by localities (TCs) then taxa, most affiliations remain a puzzle (Grauvogel-Stamm & Anderson J.M. 1980, unpublished notes).

Dordrechtites, an allochthonous vagrant

There is a marked, though not exclusive, correlation between *Dordrechtites* and more well-bedded, lower-flow-regime deposits (most notably Bir 111 and Aas 411) on the one hand, and between *Telemachus* and more poorly laminated, higher-flow-regime deposits (most notably Tel 111 and Kan 112) on the other.

The most likely resolution, as we expressed in Cairncross *et al.* (1995), is as follows: 'It is significant that *Dordrechtites* is a winged scale, apparently adapted for wind (and water) dispersal, and that these scales are invariably detached and usually scattered through a deposit. They almost certainly represent communities growing some distance removed from the site of deposition. *Telemachus*, on the other hand, is a 5–6 cm long woody cone, often found intact or partially intact, although isolated scales are also common. They appear mostly to have undergone little transportation and to have been derived from the coniferous community closely adjacent to, or within the site of deposition.'

Australia (Moolayember Fm.)

The depositional environment of the Moolayember Fm. is interpreted as a fairly extensive, inland, fluviatile-lacustrine basin with some evidence of intermittent brackish and ephemeral marine incursions (Playford *et al.* 1982). The *Dordrechtites* material derives from a single TC ('locality') and consists of 'at least 120 seeds attached to cupules, one broken cone ...., and an indistinctly preserved broken cone'. We recognise, in addition, the 'gymnosperm stem' illustrated by Playford *et al.* (1982, pl. 2, f. 4) as the axis of a *Dordrechtites* strobilus with numerous short pedicels.

The associated flora, as reflected in Playford *et al.* (1982), consists of stems and foliage of a single species of horsetail, four genera and species of fern, *Dicroidium* (two fragments), *Linguifolium* (a single fragment), *Ginkgoites* (one individual), a few other ginkgophyte fragments, *cf Rissikia* (four leafy shoots) and some fair-sized fragments of leafless gymnospermous stem. Gymnosperm fruit, aside from *Dordrechtites*, consist of *Umkomasia* (a few individuals, with one fairly complete strobilus) and *Pteruchus* (one fragment). The content and preservation of this assemblage, with the intact *Dordrechtites* and *Umkomasia* strobili and the gymnosperm stem fragments, suggests near autochthony and relatively rapid burial.

One of us (HMA, 1988) had the opportunity of studying the original collection—housed in the Dept. of Geology & Mineralogy, University of Queensland, Brisbane—and observed numerous *Heidiphyllum* leaves on slabs from this locality. These leaves were neither described nor specifically illustrated in Playford *et al.* (1982), though two fragmentary specimens do appear on the slab (pl. 6, f. 6) showing the partially intact *Dordrechtites dikeressa* cone.

The Spring Creek TC, then, like many Molteno TCs, yields the *Dordrechtites/Heidiphyllum* rather than the *Telemachus/Heidiphyllum* association of taxa, but does not contribute towards resolving the *Dordrechtites* affiliation dilemma. No other vegetative element in the flora appears to be a likely affiliate of *Dordrechtites*.

South America (Los Rastros Fm.)

Further evidence of *Dordrechtites* found in association with *Heidiphyllum*, was noted by HMA (23-09-1999) at the Aqua de la Pena locality, Ischigualasto, where a bedding plane was found literally covered with specimens of the two genera.

Intactness of cones

The overwhelming majority of *Dordrechtites* specimens are preserved as isolated scales. They obviously separate readily from the stout pedicels to which they are attached in fascicles of three or four. The proportion of dispersed single scales to scale clusters or partial strobili in the deposits, is far higher than is evident in the table—which reflects curated material only, not counts on site. For those TCs with more numerous *Dordrechtites* remains (e.g. Lut 311, Aas 311, Aas 411), the collection is strongly biased towards scale clusters (from one or more cones) and cone fragments. These are preferentially retained, while a great number of lesser preserved single scales are discarded.

It is difficult to discern any revealing pattern between the occurrence of scale clusters or cone fragments and habitat/TC type. Aas 411 (a lake deposit) is the top fruit-yielding TC in the Molteno with 13 genera of ovulate fruit, some of which are notably intact, including three specimens of *Dordrechtites*. Bir 111 (the other prolifically fossiliferous lake deposit) with six ovulate cone genera has yielded almost exclusively dispersed scales. Aas 311 and Lut 311, each with a single cone fragment, a couple of scale clusters and numerous single scales, represent low-diversity *Heidiphyllum* thickets. Kon 111 and Win 111, the additional two TCs with relatively high proportions of scale clusters, likewise represent low-diversity *Heidiphyllum* thickets.

Cuticles

Potential sample: Lit 111, *ca* 50 dispersed scales; Umk 111, 10 scales.

Macerated (this work): Lit 111, 5 scales.

Preservation grade: Grade 2 (see JSM results below).

Diagnostic characters: cells oblong, pentagonal-hexagonal, walls gently curved; nonpapillate; stoma orientation longitudinal, anomocytic; other features absent.

Comment: in the absence of results from maceration, the Jed Scanning Microscope (5800lv) scan was attempted on two or three fragments. The features sketched and described are based on this technique.

Significance:

Classification—In its cellular features (shape, walls) and the thinness of its cuticle, *Dordrechtites* is more readily placed in the pinopsids than other classes such as the ginkgoopsids or gnetopsids. The cuticle is similar to that from the upper leaf surface of *Heidiphyllum* (p. 90), which has anomocytic stomata and elongate cells. *Rissikia* (p. 112) cuticles also have oblong cells, but the stomata are brachyparacytic and lappetate. It is certainly very unlike the cuticle of the pinopsid genus *Pagiophyllum* (p. 124) with its regularly actinocytic subsidiary cells which are strongly cutinised and lappetate. The cycadopsids cannot be ruled out, as some (e.g. *Pseudoctenis*, p. 140) also have anomocytic stomata and elongate cells. Other poorly known or unknown classes of plant may obviously enter the picture.

Affiliations—The cuticle, in being similar to that of the leaf genus *Heidiphyllum*, adds to the dilemma (p. 62) around *Dordrechtites*, in addition to *Telemachus*, being a candidate for affiliation with this leaf.

Dordrechtites dikeressa Rigby, 1982
Moolayember Fm.

Gondwana diversity

The palaeodeme from the Moolayember Fm. of Queensland clearly represents a distinct species, i.e. *D. dikeressa* Rigby 1982. The cone scales are robustly spined, a feature quite absent in the Molteno material.

tfs 1,2 from
Playford *et al.*, 1982

Adaptive radiation (Molteno diversity)

Though *Dordrechtites* is both frequent (17 TCs) and often relatively abundant (>50 individuals per TC) in the Molteno, little diversity can be readily discerned. In view of the extreme scarcity of intact strobili—all appearing very alike—this assessment is based essentially on the ovuliferous scales alone. The diagnostic features characterising the species lie in the relative shape, robustness and size of the sterile arms and fertile trunk of these scales (as preserved in lateral view).

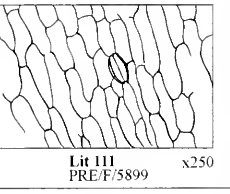
The three Molteno species are based on the following TCs/reference palaeodemes. Each derives from a distinct habitat and from a different level within the stratigraphic sequence.

D. elongatus—Aas 411 Dic/Sph (Aasvoëlberg), 100 indivs
Sphenobaiera closed woodland; Cycle 1 (Bamboesberg Member)

D. cetiparvus—Umk 111 Dic 2spp (Umkomaas Valley), 10 indivs
Dicroidium riparian forest (mature); Cycle 2b (Indwe Member)

D. mazocirrus—Maz 211 Hei/Dic (Mazenod), 40 indivs
Dicroidium riparian forest (immature); Cycle 2c (Indwe Member)

D. elongatum



sketched from Jed Scanning Microscope (5800 LV) photo

Lit 111 x250
PRE/F/5899

Dordrechtites elongatus H.M.And. 1978

Holotype
Specimen: BP/2/5283(C-Dt.II 365 in And. 1978); pl. 3(3).
Assemblage (TC): Bir 111 Sph 2spp; Birds River.
Preservation: single dehisced scale, without counterpart; impression in thinly laminated, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): Aas 411 Dic/Sph; Aasvoëlberg; pl. 1(1–8).
Specimens: >100 individuals; 2 incomplete mature strobili (tfs 2, 3 adjacent), 1 incomplete immature strobilus, *ca* 15 scale clusters of >10 dehisced scales and *ca* 15 clusters of 3–10 scales; many isolated scales.
Preservation: impressions (3D moulds/casts) in thinly laminated, strongly baked, yellowish grey shale with very good cleavage.

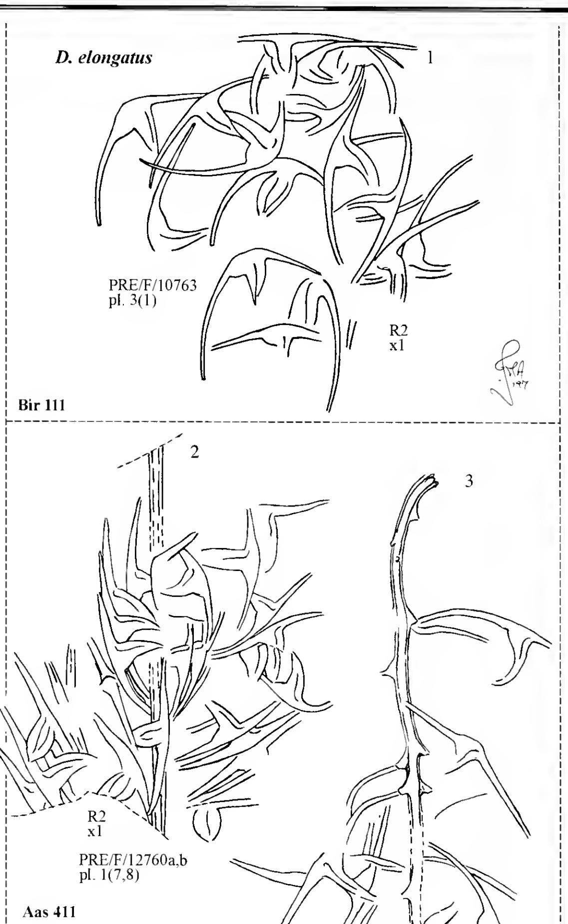
Sister palaeodemes—15 (best three listed)
Bir 111 Sph 2spp: >50 indivs (1 good scale cluster).
Lut 311 Hei/Dic: >50 indivs (1 strobilus).
Aas 311 Hei elo: >40 indivs (1 strobilus).

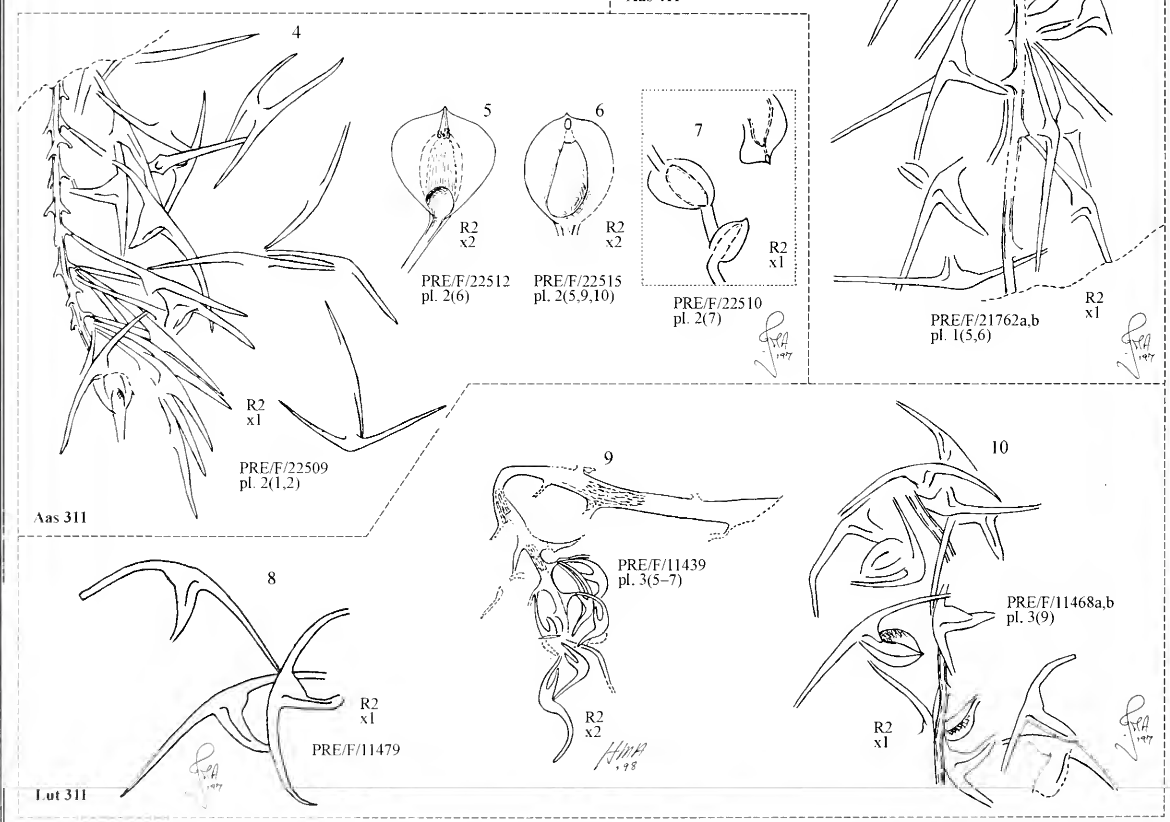
Specific diagnosis
A *Dordrechtites* species bearing relatively large scales with long, gracile, roughly equal arms and gently arching fertile trunk.

Specific characters
Ovuliferous scale: relatively large; sterile arms gracile, approximately equal (15 mm long); fertile trunk acutely conical, arching slightly proximally.

Etymology
elongatus (Lat.)—with reference to the long arms of the scale.

Comments & comparison
This is by far the most common species of *Dordrechtites*, with the scales being remarkably constant in size and shape through the 17 different TCs. It is distinct in being larger and with longer arms than both *D. cetiparvus* which is considerably smaller, and *D. mazocirrus* which has a strongly curled proximal trunk.





Dordrechtites cetiparvus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: BP/2/1129; pl. 4(1, 6).
Assemblage (TC): Umk 111 Dic 2spp; Umkomaas Valley.
Preservation: single dehisced scale, without counterpart; compression in thinly laminated, carbonaceous (good cuticle) moderately baked, dark grey shale with good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 10 indivs (all isolated scales), tfs 1–6 adjacent, pl. 4 (1–8).

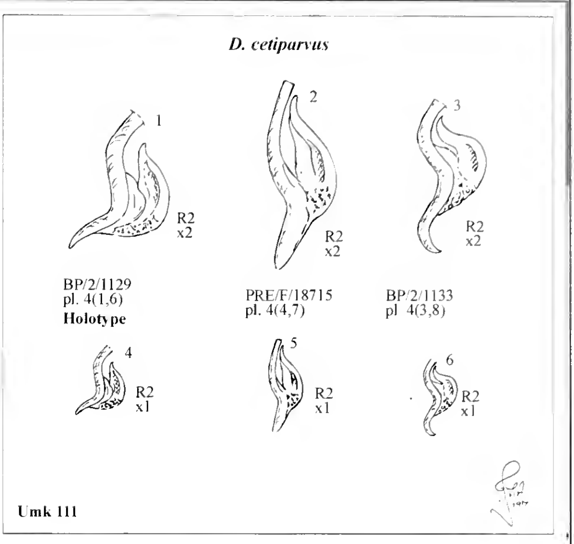
Sister palaeodemes—nil.

Specific diagnosis
A *Dordrechtites* species bearing small scales with robust, very unequal arms and sinuous, strongly reflexed fertile trunk.

Specific characters
Ovuliferous scale: small, compact; sterile arms robust, unequal, distal arm markedly shorter (*ca* 5 mm long); fertile trunk relatively robust, strongly curved proximally, sinuous towards apex.

Etymology
cetiparvus—cetus (Lat.), whale, after the locality Umkomaas (which means cow or whale in the local Zulu language); *parvus* (Lat.), small, with reference to the short arms of the scale.

Comments & comparison
The small size and curved arms of this species (known only from Umk 111) are somewhat reminiscent of the immature attached scales from Lut 311. However, as the scales are all found detached and isolated they are regarded as mature and, therefore, as a distinct species.



Dordrechtites mazocirrus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/4724a,b; pl. 4(15, 16).
Assemblage (TC): Maz 211 Hei/Dic; Mazenod.
Preservation: intact fascicle of four scales, part and counterpart; compression in thinly laminated, carbonaceous (poor cuticle) medium grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: >40 indivs (2 clusters of 3–10 scales, >38 isolated scales), tfs 7–11 adjacent, pl. 4 (9–16).

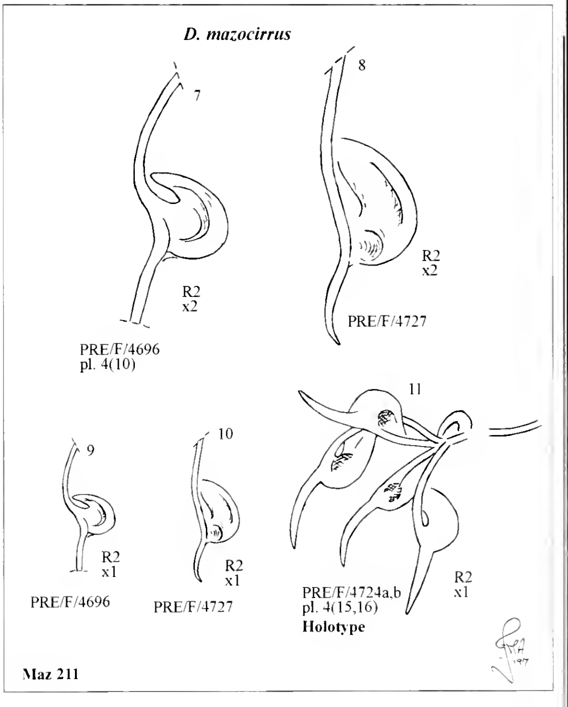
Sister palaeodemes—nil.

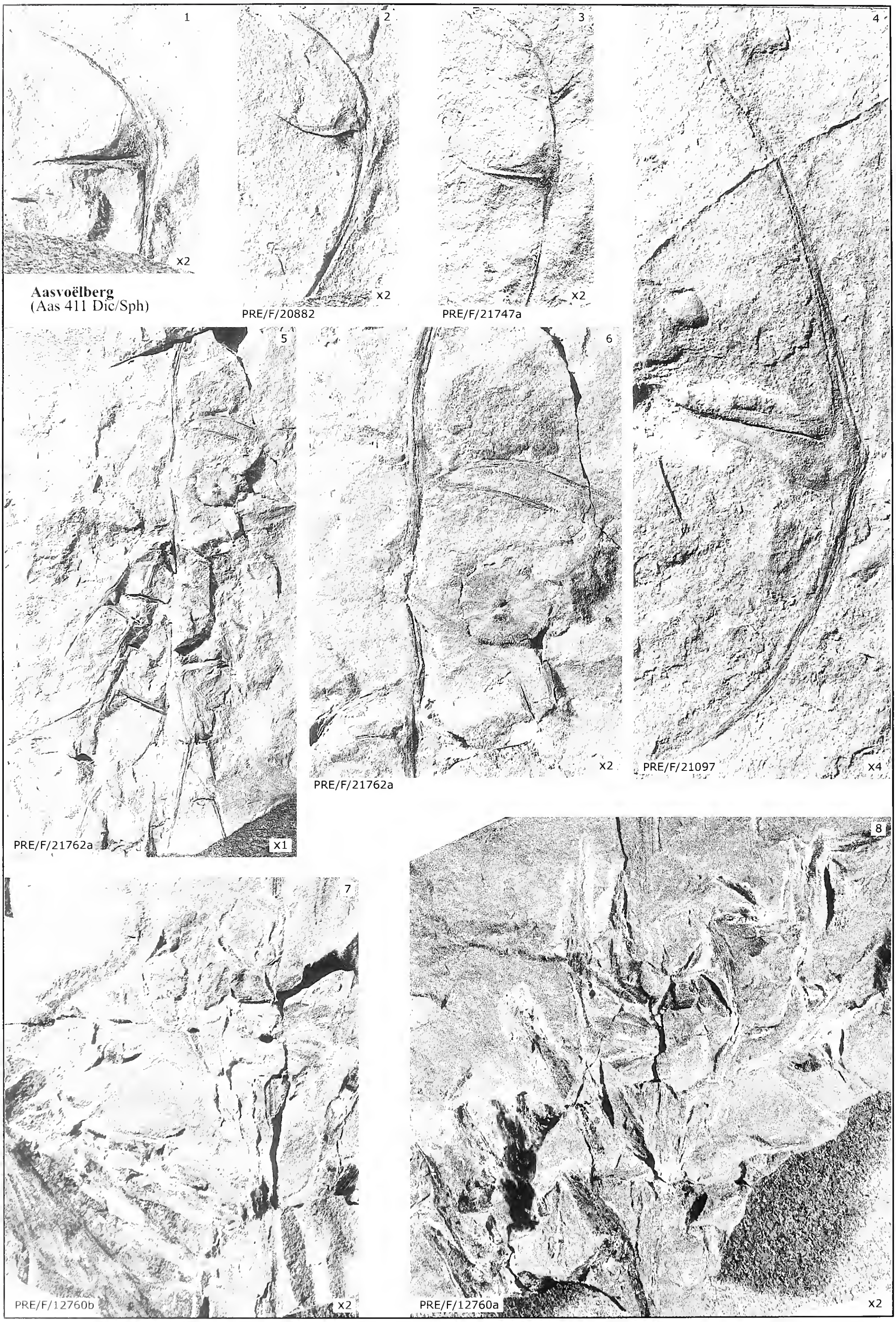
Specific diagnosis
A *Dordrechtites* species bearing relatively large scales with clearly unequal arms and full, rounded, strongly reflexed fertile trunk.

Specific characters
Ovuliferous scales: relatively large; sterile arms gracile, unequal, distal arm markedly shorter (*ca* 10 mm); fertile trunk robust, very strongly arched proximally.

Etymology
mazocirrus—mazo (Lat.), after the locality Mazenod; *cirrus* (Lat.), curl, with reference to the curled trunk of the scale.

Comments & comparison
The consistent nature of the rounded, strongly reflexed ovuliferous trunk of the scales (known only from Maz 211), makes this species quite unique.



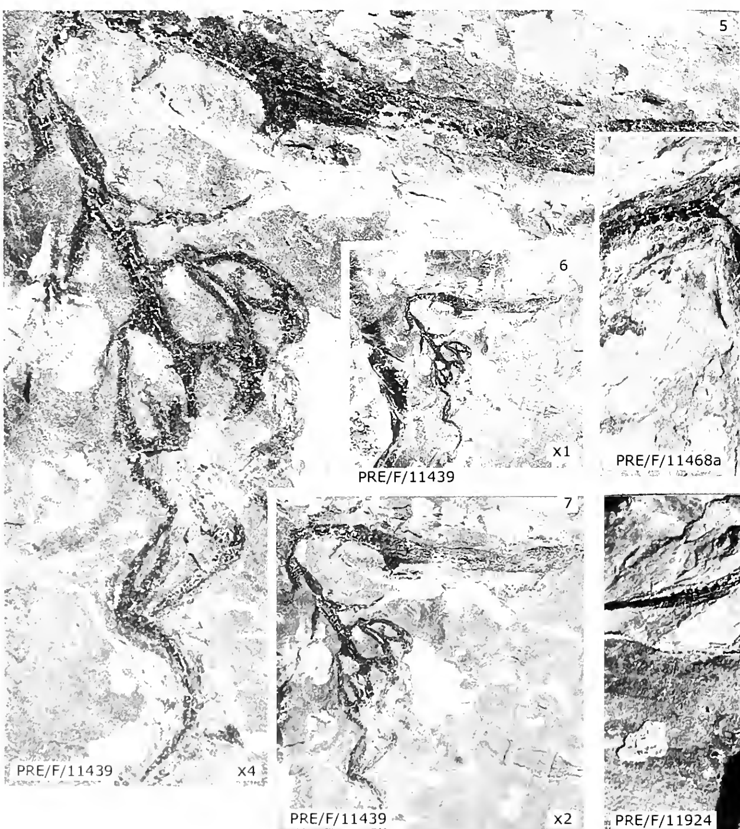


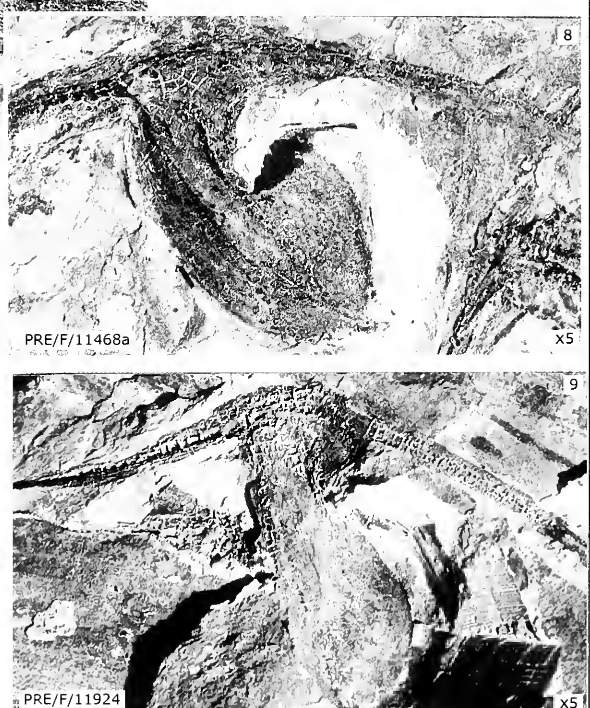
Dordrechtites elongatus **pl. 1** **DORDRECHTITALES**

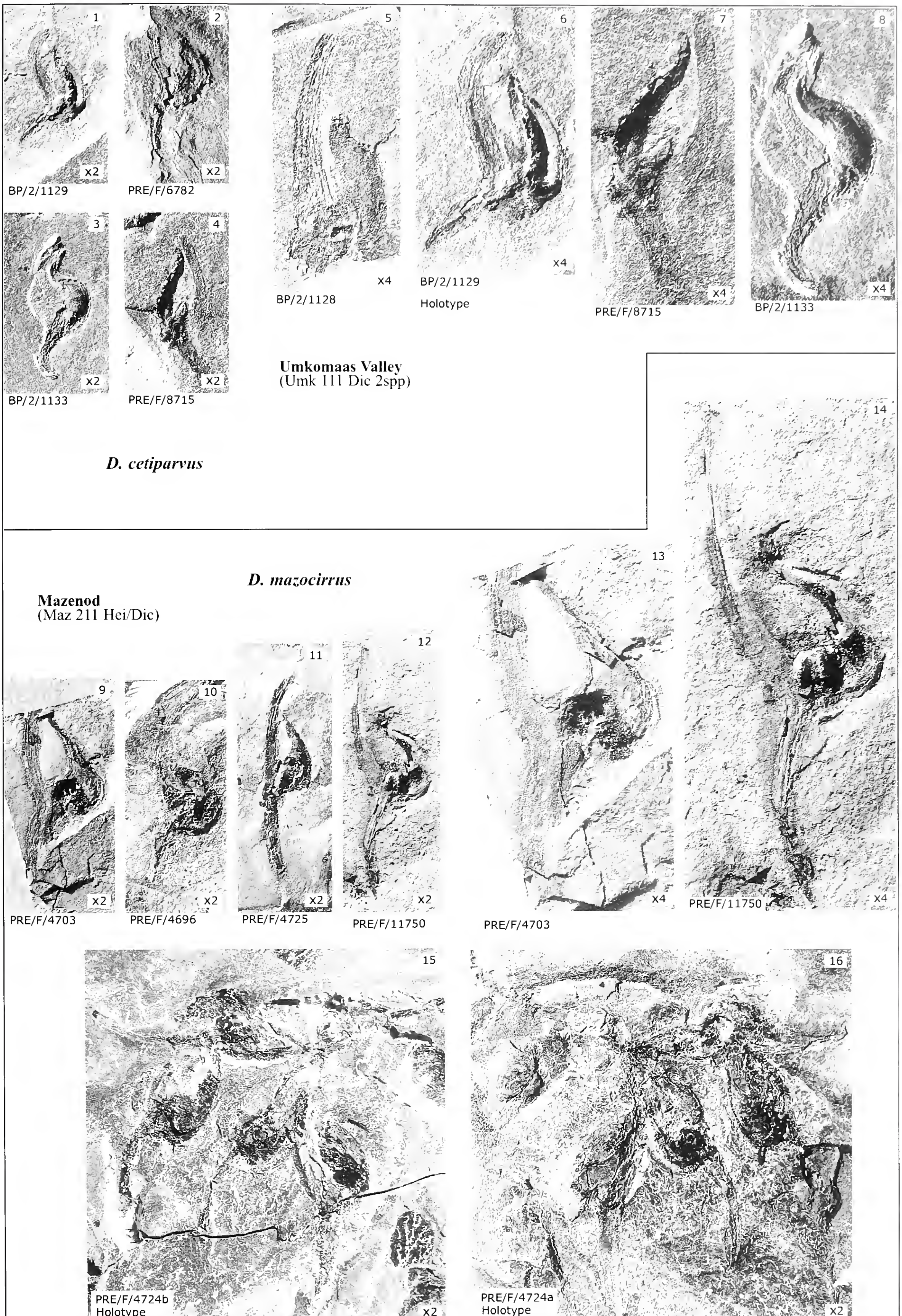
DORDRECHTITALES **pl. 2** *Dordrechtites elongatus*

Birds River
(Bir 111 Sph 2spp)

Lutherskop
(Lut 311 Hei elo)






1
x2
BP/2/1129
2
x2
PRE/F/6782
3
x2
BP/2/1133
4
x2
PRE/F/8715
5
x4
BP/2/1128
6
x4
BP/2/1129
Holotype
7
x4
PRE/F/8715
8
x4
BP/2/1133
Umkomaas Valley
(Umk 111 Dic 2spp)
D. cetiparvus
D. mazocirrus
Mazenod
(Maz 211 Hei/Dic)
9
x2
PRE/F/4703
10
x2
PRE/F/4696
11
x2
PRE/F/4725
12
x2
PRE/F/11750
13
x4
PRE/F/4703
14
x4
PRE/F/11750
15
PRE/F/4724b
Holotype
x2
16
PRE/F/4724a
Holotype
x2

PINOPSIDA S.V.Meyen 1984
VOLTZIALES J.M.And & H.M.And., ord. nov.
INCERTAE SEDIS family

Fredianthus J.M.And. & H.M.And., gen. nov.

Type species
Fredianthus maysiformis J.M.And. & H.M.And., sp. nov.

Generic diagnosis
A voltzialean male cone of very large size (*ca* 220 mm long) with strongly sigmoidal microsporophylls bearing a single row of *ca* 5 abaxial clusters (*ca* 9 sacs each) of microsporangia.

Generic characters
Strobilus: a compact cone, lanceolate, of very large size (*ca* 220 x 53 mm as reconstructed); axis stout (*ca* 11 mm diam.), moderately flexed; microsporophylls helically attached, in *ca* 60 gyres of *ca* 25–30 units.
Microsporophyll: a simple scale, proportionately long, strongly sigmoidal, at 90° from axis; distal lamina leafy, narrowly ovate, margin deeply dentate with *ca* 12 lobes, without heel; stalk terete, narrow (*ca* 1 mm diam.); microsporangia numerous (*ca* 45), abaxial, in a single median row of *ca* 5 clusters, each with *ca* 9 radiating pollen sacs borne on a short pedicel.
Microsporangium: elliptical (2 x 1 mm), retuse with clear, central, longitudinal line (dehiscence slit?).
Pollen: unknown.

Eponymy
Fredianthus—in honour of Fred Terblanche, farmer at Goedehoop who first showed us the type locality and has, more than once, aided excavation with his tractor and ripper.

Global Range: Gondwana, Tr. (CRN).
First & last: the single Molteno species described here.

Gondwana Triassic occurrence
SAf—Karoo Basin, 1 TC (2 indivs).

Molteno occurrence
Frequency (F): 1 TC (of 100 sampled in the Molteno).
Diversity (D): 1 species.
Abundance (A): 2 individuals total.
Aas 411: 2 indivs in 512 man-hrs cleaving (1 per 25 man-days) extremely rare

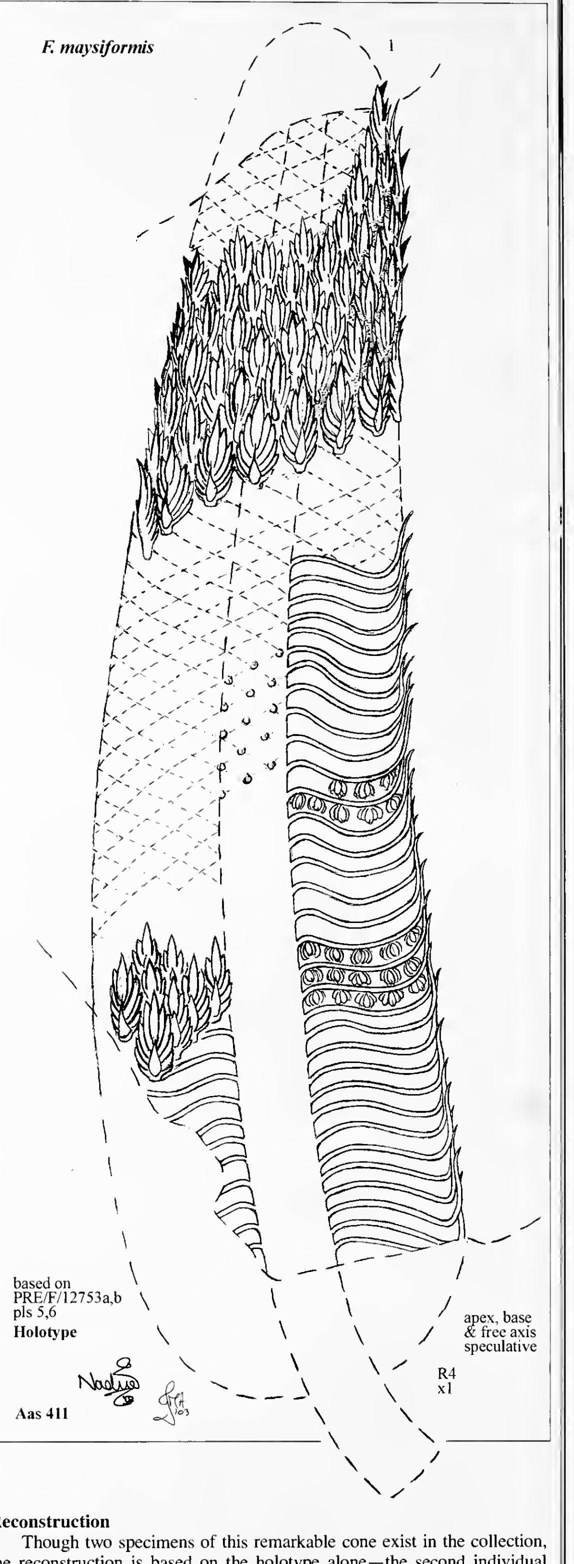
Affiliated organs
Female: unknown.
Foliage: unknown.

With 13 ovulate genera recorded (Tab. 11, p. 15), Aasvoëlberg (Aas 411) is the richest fruit-yielding TC in the Molteno. Yet there occurs at the site no obvious ovulate coniferopsid cone that might affiliate with *Fredianthus. Dordrechtites,* without a known affiliate, must be considered a remote possibility.

A similar problem arises with regard to a foliage affiliate. Three coniferopsid genera—*Heidiphyllum* (1%), *Rissikia* (25 individuals) and *Pagiophyllum* (two small fragments)—occur in the assemblage, none of which is a likely candidate. *Heidiphyllum* and *Rissikia* are preoccupied, while *Pagiophyllum* (known nowhere else in the Molteno) is considered to belong to the order Pinales and not the more primitive Voltziales.

Classification & comparison
Suprageneric classification (family Incertae/Voltziales)
Fredianthus is placed in the Voltziales—transitional between the Cordaitanth.ales and Pinales—though it is quite unlike any of the Laurasian male cones included in the order (pp. 57, 59). It is perhaps most readily derived from a form such as the Siberian Permian genus *Cladostrobus* (Rufloriaceae, Cordaitanthales, tf. 25, p. 59). In view of the lack of any established affiliation with ovulate cones or foliage, *Fredianthus* is not included in any formal family. However, considering its unique size and arrangement of microsporangia, it probably represents a new group at this rank.

Intergeneric comparison (Molteno genera)
Odyssianthus and *Lutanthus*, sister genera of *Fredianthus* in the Molteno, are judged sufficiently distinct—given what is currently known of male conifer cones—to represent separate families within the Voltziales (Tab. 30, p. 54). See Tab. 31 (p. 57) for a possible resolution of the relationships between the male pinopsid cones from the later Carboniferous to Triassic.



Reconstruction
Though two specimens of this remarkable cone exist in the collection, the reconstruction is based on the holotype alone—the second individual being a small, poorly preserved fragment. The apex and base of the cone, being unknown, are conjecture. The number of scales per gyre, the distal lamina and the arrangement and number of microsporangia are a best attempt at interpretation, the security of which will clearly increase with more and better preserved material. In view of the extreme rarity of the taxon, however, the gathering of additional specimens is not too likely in the near future.

Fredianthus maysiformis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/12753a,b; pl. 5(1–4), pl. 6(1–7).
Assemblage (TC): Aas 411 Dic/Sph; Aasvoëlberg.
Preservation: part and counterpart of a fairly complete cone (175 x 55 mm); apex and proximal end with stalk missing; preserved primarily in longitudinal section with outer face of scales seen only in variable side view along cone margin; microsporangia *in situ* and undehisced throughout; impression in thinly laminated, strongly baked, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 2 individuals; including the holotype and an additional small cone fragment.

Sister palaeodemes—nil.

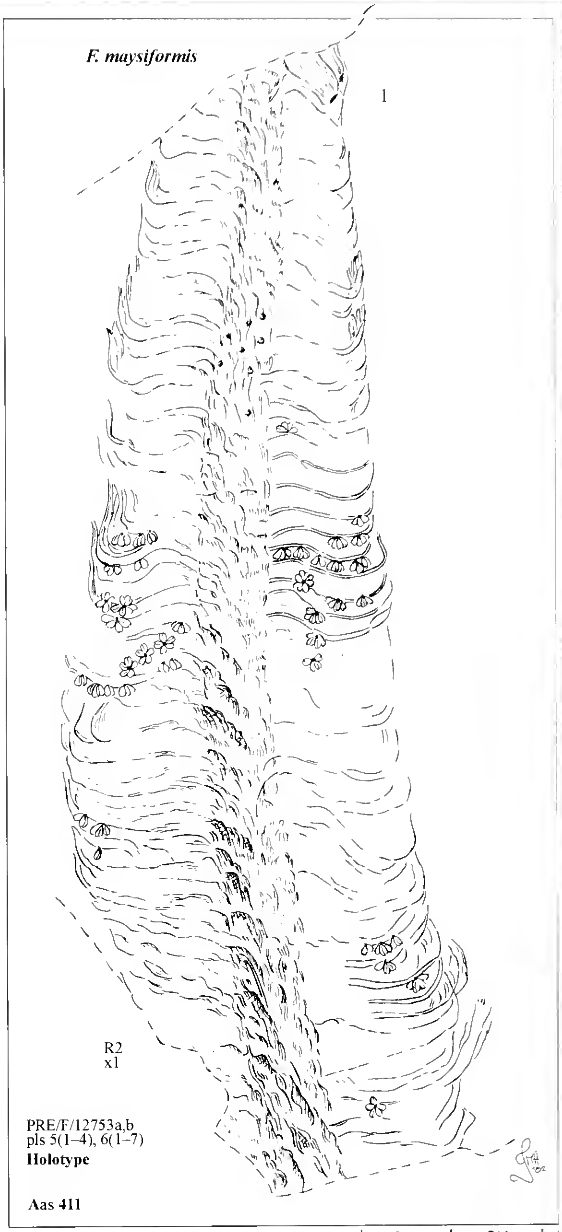
Specific diagnosis—as for genus.

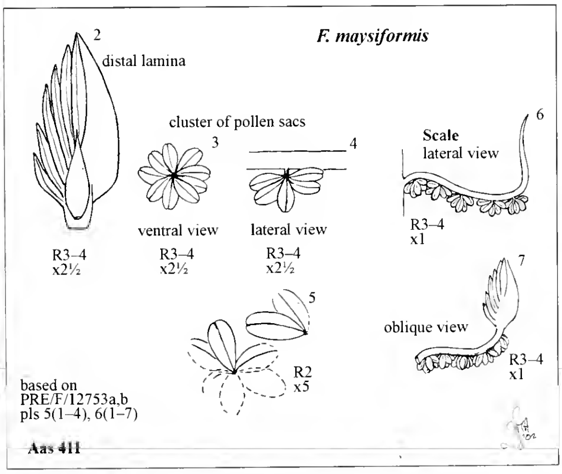
Specific characters—as for genus.

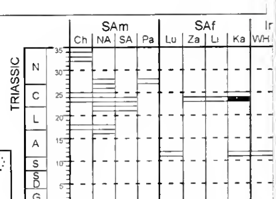
Etymology
maysiformis—with reference to the superficial similarity to a maize (corn, mealie) cob.

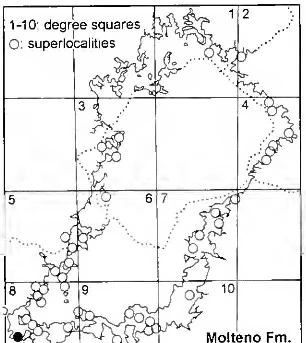
Classification & comparison
Fredianthus maysiformis, at *ca* 200 mm length, appears to be the largest Pinopsida male cone—fossil or extant—yet recorded. In the extant Coniferales, the male cones are generally small (30 mm long or shorter) and the sporangia few in number. Throughout the Pinaceae there appear only two sporangia, and in most other extant families from two to seven sporangia. The largest male cone (*Araucaria bidwilli*) reaches a length of 120 mm and the highest number of sporangia per sporophyll (in *Agathis*) is 13–15 (Foster & Gifford 1974).

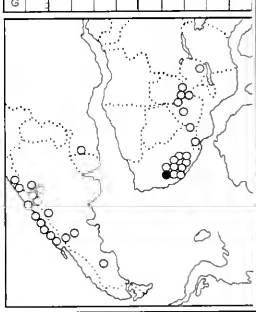
In contrast, the Cycadales bear numerous sporangia (30 in *Zamia* to >1 000 in *Cycas*) and have characteristically large male cones (>200 mm). A very large cone (200 mm long), presumed to be female, is recorded from the Burgersdorp Fm. as *Sewardistrobus* (And. & And. 1985).

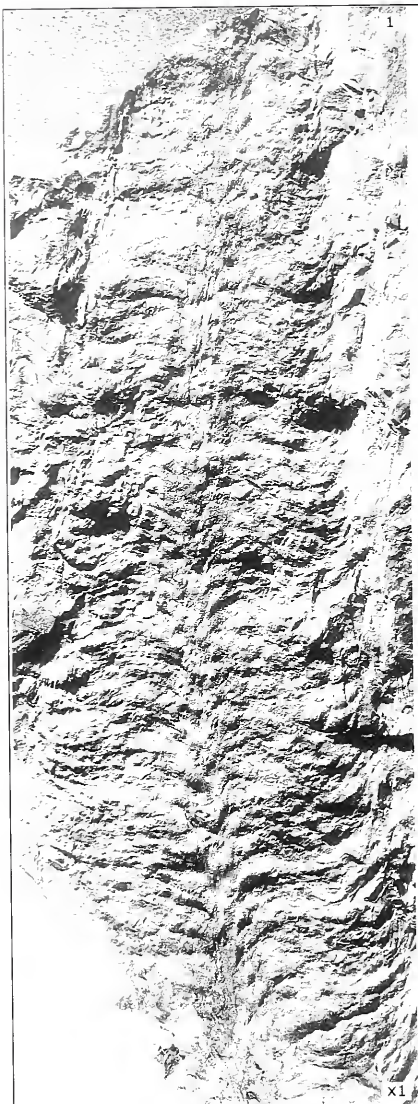


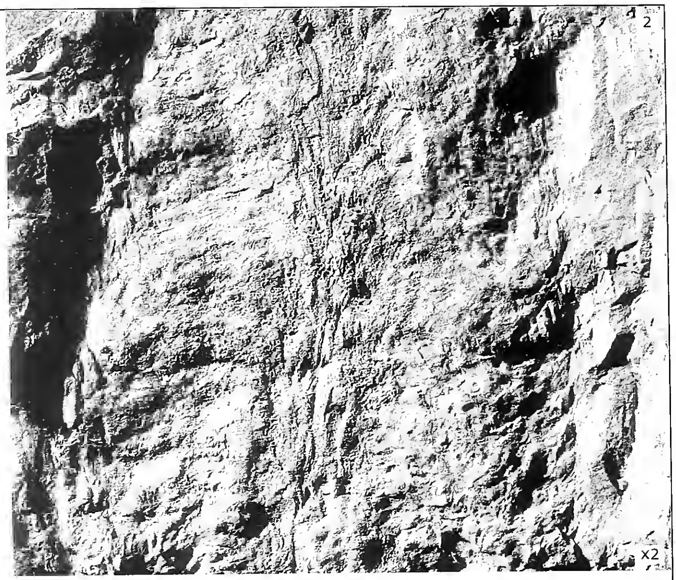






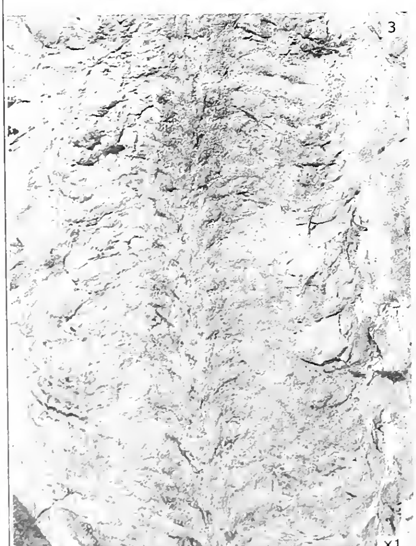


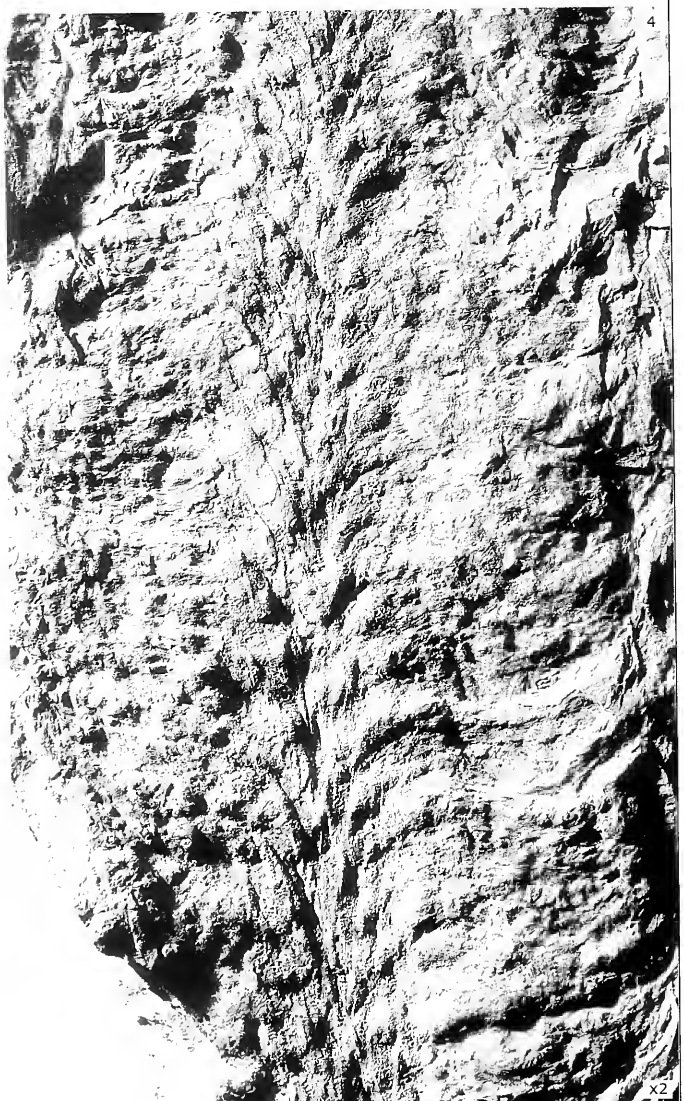


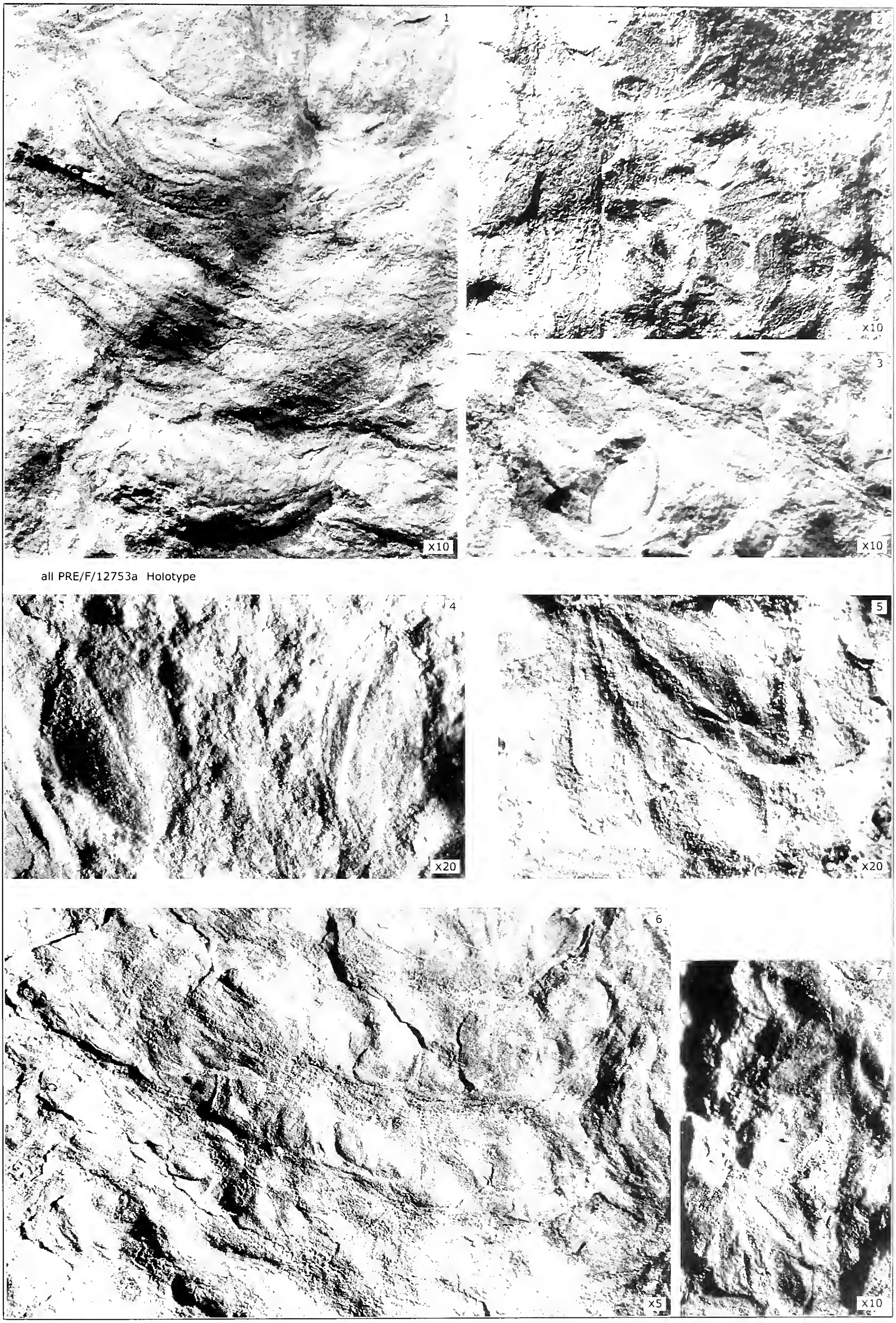


all PRE/F/12753a Holotype

Aasvoëlberg
(Aas 411 Dic/Sph)







all PRE/F/12753a Holotype

PINOPSIDA S.V.Meyen 1984
VOLTZIALES J.M.And. & H.M.And., ord. nov.
INCERTAE SEDIS J.M.And. & H.M.And., fam. nov.

Lutanthus J.M.And. & H.M.And., gen. nov.

Type species
Lutanthus hemidiscus J.M.And. & H.M.And., sp. nov.

Generic diagnosis
A voltzialean male cone of small size (*ca* 30–40 mm long) with straight to moderately upcurving microsporophylls bearing few microsporangia (6–8) in diverse modes of attachment.

Generic characters
Strobilus: a compact cone, oblong-elliptic, apex rounded, base truncate, of relatively small size (*ca* 30–40 mm long); axis stout to very stout, strongly flexed to erect, without free base (cone sessile); microsporophylls helically attached, number of gyres (13–24) and units per gyre (10–20) very variable.
Microsporophyll: a simple scale, proportionately short, curving upward distally, at 45° to 90° from axis; distal lamina leafy, ribbed to lobed to hemispherical and entire, without heel; stalk narrow to broadly tapering, variously winged; microsporangia few in number (6–8), adaxial to abaxial, in 1 or 2 rows, clustered or single, sessile.
Microsporangium: variously obovate to elliptical or rhomboidal (*ca* 1 mm long), generally with a clear longitudinal (?)dehiscence slit.
Pollen: unknown.

Etymology
Lutanthus—after the type locality, Lutherskop.

Global Range: 3 spp., Gondwana, Tr. (CRN).
First & last: the three Molteno species described here.

Gondwana Triassic occurrence
SAf—Karoo Basin, 3 TCs (5 indivs).

Molteno occurrence
Frequency (F): 3 TCs (of 100 sampled in the Molteno).
Diversity (D): 3 species.
Abundance (A): 5 individuals total, very rare to vanishingly rare.

Gre 111 Equ sp:	2 indivs in	25 man-hrs cleaving	(1 per	1 man-day)	very rare
Lut 311 Hei elo:	2 "	" 50 "	" (1 "	$2^1/_2$ ")	very rare
Aas 411 Dic/Sph:	1 "	" 512 "	" (1 "	51 ")	vanish. rare

This pattern of scarcity recorded for *Lutanthus* is consistent with that noted for the other Molteno voltzialean male cones, *Fredianthus* and *Odyssianthus*.

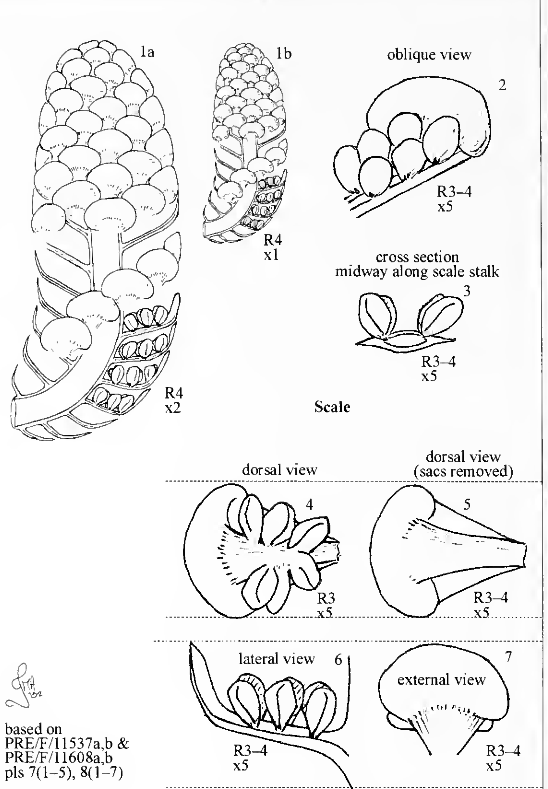
Affiliated organs
Female cone: unknown.
Foliage: unknown.

Though we recognise in the Molteno only a single genus each of voltzialean foliage (*Heidiphyllum*) and female cone (*Telemachus*), there appear to occur, in the very scarce material at hand, at least three genera of male cone. For neither *Lutanthus* or *Fredianthus* are there further foliage or female taxa (in the Pinopsida) in the collections for suggesting possible affiliations.

Classification & comparison
Suprageneric classification (Incertae Sedis/Voltziales)
Lutanthus, along with its two Molteno sister genera, *Fredianthus* and *Odyssianthus*, is included, with considerable reservation, in the order Voltziales (see discussion on pp. 70, 88). In the absence of affiliated ovulate cones or foliage, the genus is placed as family incertae sedis. It would be quite feasible to derive *Lutanthus* from the Late Permian glossopterid microsporangiate genus *Lidgettonia* as depicted in Tab. 31 (p. 57) and noted on p. 56—offering a wholly different polyphyletic pinopsid phylogeny.

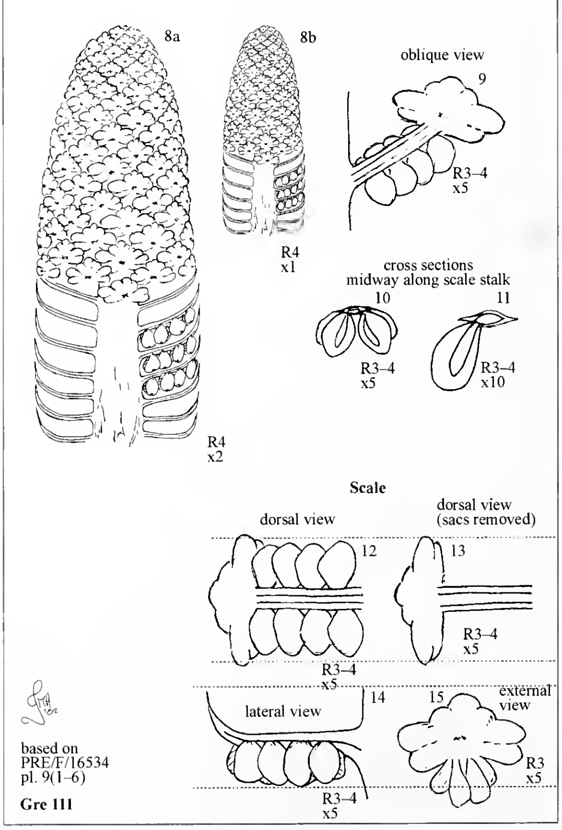
Intergeneric comparison (Molteno genera)
In what measure do the three Molteno voltzialean male cones, *Lutanthus*, *Fredianthus* and *Odyssianthus*, differ? They are represented by a total of only nine individuals and could conceivably, at one end of the spectrum of possibilities, be placed in a single genus. The fact that the Molteno voltzialean foliage is confined almost exclusively to the highly dominant genus *Heidiphyllum* tends to support this option. We favour the three-genera alternative, however, for the reasons best clarified in the text, tables and comparative figures on pinopsid phylogeny and morphology, pp. 56–59. Indeed, we find it most plausible within the context of the great Triassic radiation that three distinct families, possibly even orders, might be represented.

L. hemidiscus

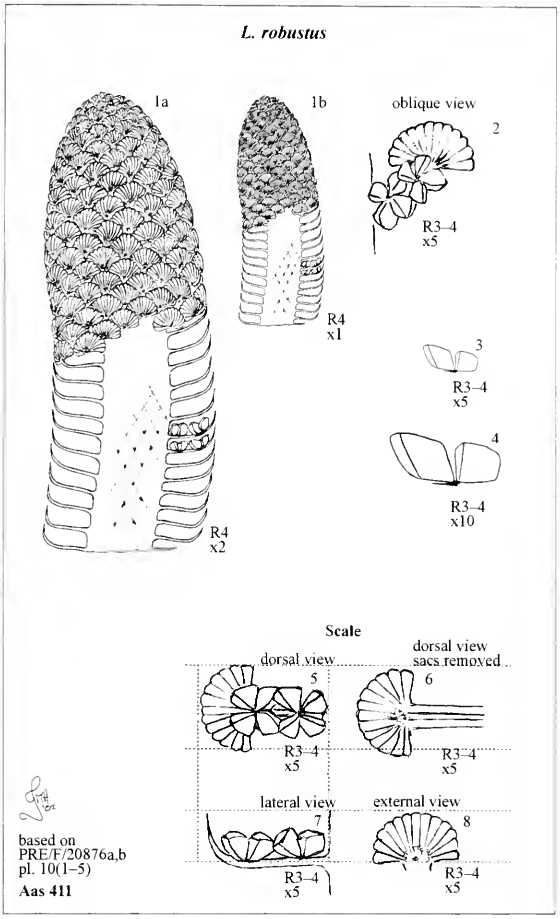


based on PRE/F/11537a,b & PRE/F/11608a,b pls 7(1–5), 8(1–7)
Lut 311

L. ornatus



based on PRE/F/16534 pl. 9(1–6)
Gre 111



	assemblages (taphocoenoses)	♂ *Fredianthus*	♂ *Lutanthus*	♂ *Odyssianthus*	♂ *Rissikianthus*	♂ *Helvetianthus*
1	Gre 111 Equ sp	-	2	-	-	-
2	Boe 112 Dic cor	-	-	-	1	-
3	Tel 111 Hei elo	-	-	2	-	-
4	Lut 311 Hei elo	-	2	-	-	-
5	Pen 321 Dic/Ris	-	-	-	30	-
6	Kap 111 "	-	-	-	25	-
7	Umk 111 Dic 2spp	-	-	-	8	-
8	Lit 111 Dic/Hei	-	-	-	-	6
9	Aas 411 Dic/Sph	2	1	-	15	-
Total TCs		1	3	1	5	1
Total indivs		2	5	2	79	6

Tab. 34. Pinopsid pollen cone genera, Molteno occurrence

Matrix: curated individuals in collection
Frequency/abundance: aside from *Rissikianthus*, it is clear that pinopsid pollen cones are rarely encountered

Reconstructions

The R4 reconstructions of the three *Lutanthus* species portrayed here are variously secure; based as they are on so few (five in total) individuals. It is most particularly in the arrangement and attachment of the microsporangia that the uncertainties lie. Settling decisively on the critical question of adaxial or abaxial emplacement has proved notoriously tricky for all three species. The options as illustrated and described seem most likely, but are not certain. To summarise: the microsporangia in the three species appear to range from being attached in two latero-abaxial rows (in *L. ornatus*), to two latero-adaxial rows (*L. hemidiscus*), to a single adaxial row (*L. robustus*). If one allows for the lateral wings of the stalks being suppressed and a small degree of adaxial migration of the two rows of microsporangia in the first two species, then a similar morphological condition in the three species can be visualised. The trio of species being related at generic level is conceivable (but see also text adjacent).

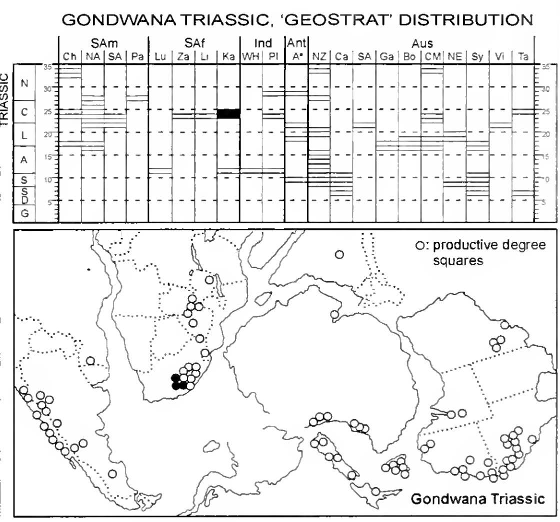
From the material at hand (pls 78–81), which lacks any evidence of free axes, we take all three species to be sessile.

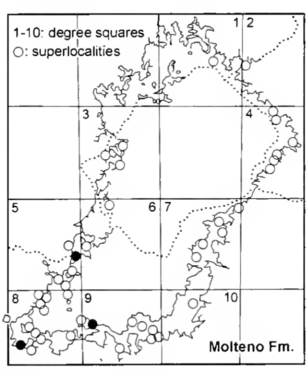
Adaptive radiation

The rather disparate group of three species from three different Molteno localities is brought together into the single genus *Lutanthus* with obvious uncertainty since the material is so scarce and none of it is completely or explicitly enough preserved to render all diagnostic features unambiguous. The differences between the three species are so marked that we might well be dealing with three distinct genera; but if so, where are their foliage and female affiliates? The most diagnostic features differentiating the species are seen in the various elements of the scales—distal lamina, stalk and pollen sacs.

The three Molteno species are based on the following TCs/reference palaeodemes. Each derives from a very distinct habitat and from a different member within the stratigraphic sequence.

L. hemidiscus—Lut 311 Hei elo (Lutherskop); 2 indivs
Heidiphyllum thicket; Cycle 3 (Mayaputi Member)
L. ornatus—Gre 111 Equ sp. (Greenvale); 2 indivs
Equisetum marsh; Cycle 4/5 (Qiba Member)
L. robustus—Aas 411 Dic/Sph (Aasvoëlberg); 1 indiv
Sphenobaiera closed woodland; Cycle 1 (Bamboesberg Member)





Lutanthus hemidiscus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/11537a,b; pl. 7(1–5).
Assemblage (TC): Lut 311 Hei elo; Lutherskop.
Preservation: fairly complete cone, part and counterpart, longitudinal outer view with several scales and numerous microsporangia clearly evident; impression in thickly laminated, medium grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 2 indivs (tfs 1, 2 opposite).

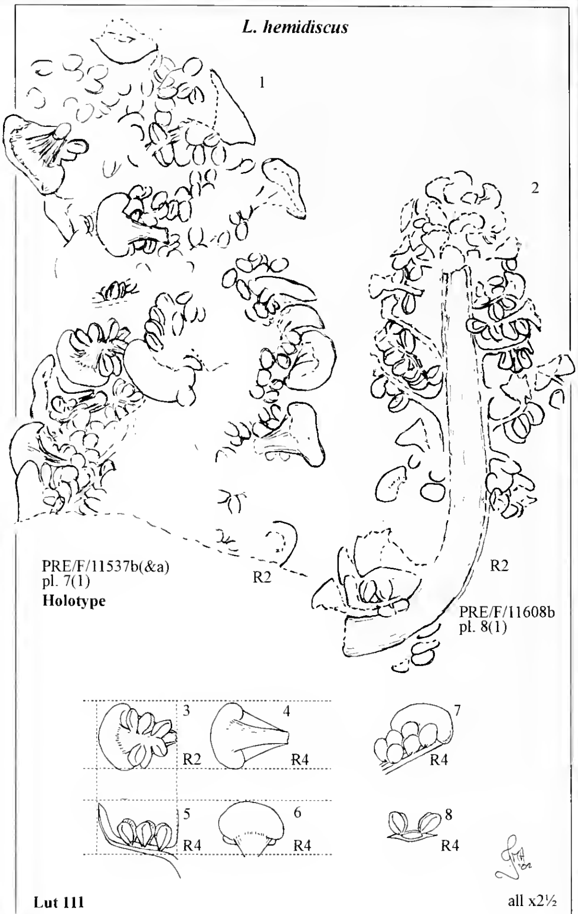
Sister palaeodemes—nil.

Specific diagnosis
A *Lutanthus* cone with strongly flexed axis, large hemispherical scales, and microsporangia with distinctive (?)dehiscence line.

Specific characters
Strobilus: axis moderately stout, strongly flexed to base; microsporophylls in *ca* 13 gyres of *ca* 10–12 units.
Microsporophyll: distal lamina large, hemispherical, margin entire; stalk broad, spreading distally, widely winged; microsporangia adaxial, dorsolaterally attached to midrib, single, sessile, in two irregular rows of 3 or 4 pollen sacs.
Microsporangium: *ca* 1.1 mm long, variously obovate to elliptical, occasionally kidney-shaped; with distinct (?)dehiscence line running full length.

Etymology
hemidiscus (Lat.)—half disc, with reference to the shape of the scale.

Comment & comparison
With two relatively complete individuals from Lut 311, the holotype seen in rather disarticulated outer view, the sister specimen in section, *L. hemidiscus* is the best known of the three *Lutanthus* species and is the obvious choice as type species for the genus. Its conspicuous, hemispherical scale laminae with entire margins are particularly characteristic.



Lutanthus ornatus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/16534; pl. 9(1–6).
Assemblage (TC): Gre 111 Equ sp.; Greenvale.
Preservation: nearly complete cone (proximal end missing), without counterpart, longitudinal outer view and part section, with a couple of scales and numerous microsporangia clearly evident; impression in thickly laminated, medium grey shale with good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 2 indivs (tfs 9, 10 opposite).

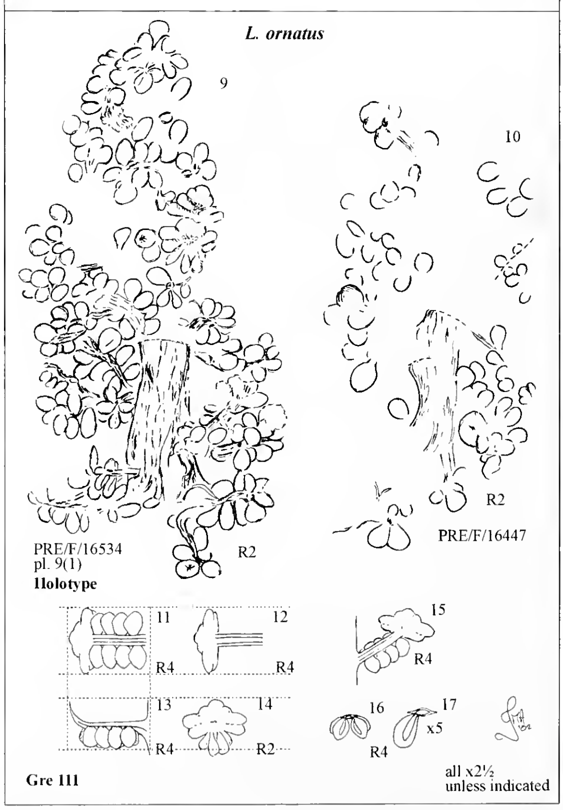
Sister palaeodemes—nil.

Specific diagnosis
A *Lutanthus* cone with straight axis, distinctively lobed scales, and ornamented microsporangia with clear 'micropyle'.

Specific characters
Stobilus: axis moderately stout, expanding strongly to base, not flexed; microsporophylls in *ca* 17 gyres of *ca* 15 units.
Microsporophyll: distal lamina fairly large, distinctively multilobed; stalk linear, narrowly winged; microsporangia abaxial, ventrolaterally attached to midrib, single to semiclustered, sessile, in 2 rows of *ca* 4 pollen sacs.
Microsporangium: *ca* 1.1 mm long, obovate, oval to circular in end view; with distinct linear-obovate (?)dehiscence line running most of length; and a distinctive, linear cellular ornamentation radiating out from apical 'micropyle'.

Etymology
ornatus (Lat.)—with reference to the ornamented microsporangia.

Comment & comparison
L. ornatus, with its clearly ornamented microsporangia and well-lobed scales, is as distinctive a species as *L. hemidiscus*. The lobed scale laminae are, however, confusingly camouflaged amongst the mass of pollen sacs in the two available specimens. It is the difference in ornamentation between lamina and sacs, as seen under the microscope, that sets these two elements of the cone apart.



Lutanthus robustus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/20876a,b; pl. 10(1–5).
Assemblage (TC): Aas 411 Dic/Sph; Aasvoëlberg.
Preservation: Fairly complete cone (proximal end missing), part and counterpart, longitudinal section showing numerous scales and a scatter of *in situ* microsporangia; impression, imperfectly preserved; impression in thinly laminated, strongly baked, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 1 indiv. (tf. 1 opposite).

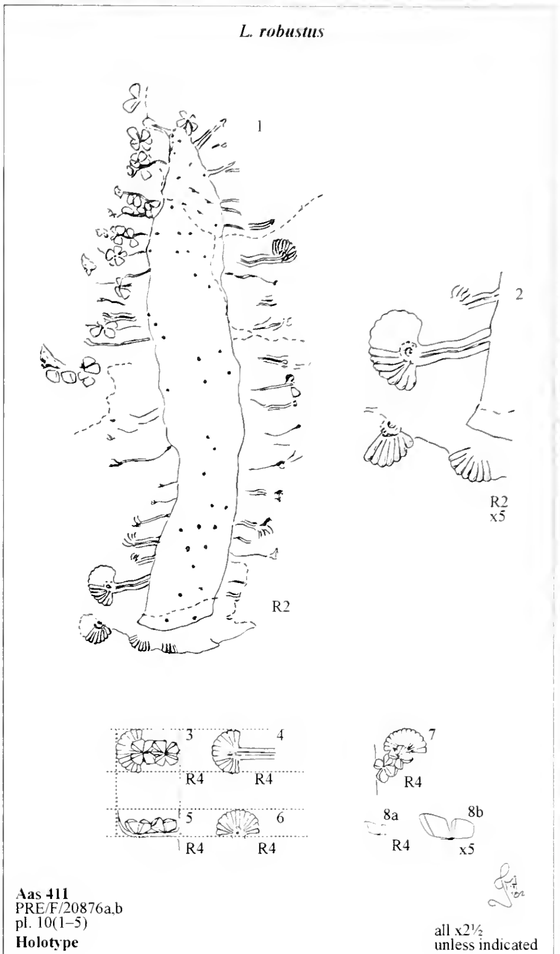
Sister palaeodemes—nil.

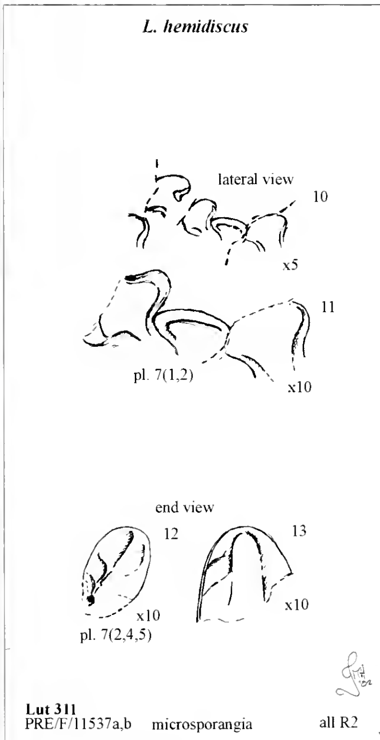
Specific diagnosis
A *Lutanthus* cone with gently flexed robust axis, small ribbed scales, and rhomboidal microsporangia without distinctive features.

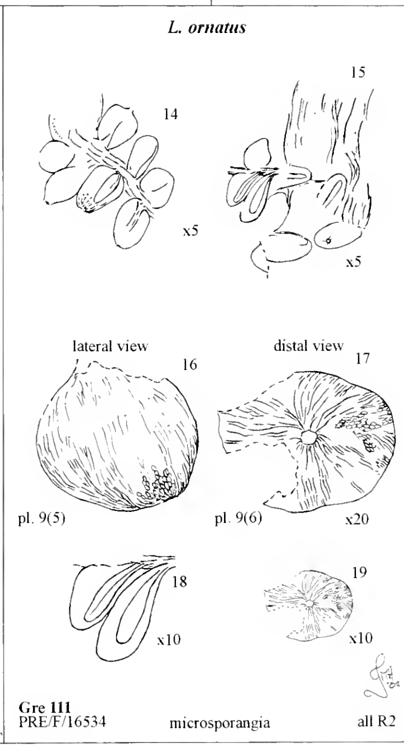
Specific characters
Strobilus: axis markedly robust, very gently flexed to base; microsporophylls in *ca* 24 gyres of *ca* 20 units.
Microsporophyll: distal lamina relatively small, kidney-shaped, multiribbed, margin dentate-crenate; stalk linear, moderately winged; microsporangia adaxial, dorsally attached to midrib, in 2 sessile radiating clusters of 4 or 5 pollen sacs.
Microsporangium: *ca* 0.8 mm long, irregularly rhomboidal; with no evident mode of dehiscence or ornamentation.

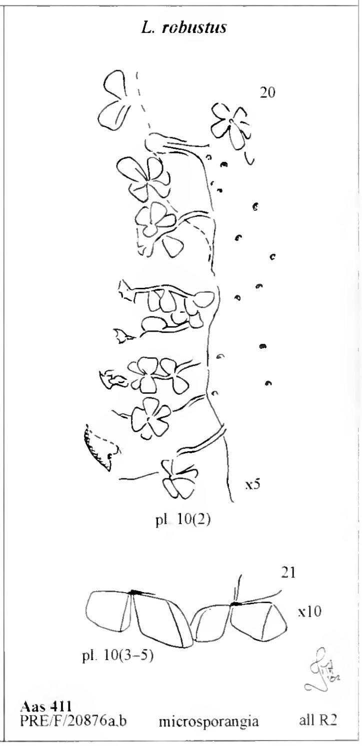
Etymology
robustus (Lat.)—with reference to the stout axis.

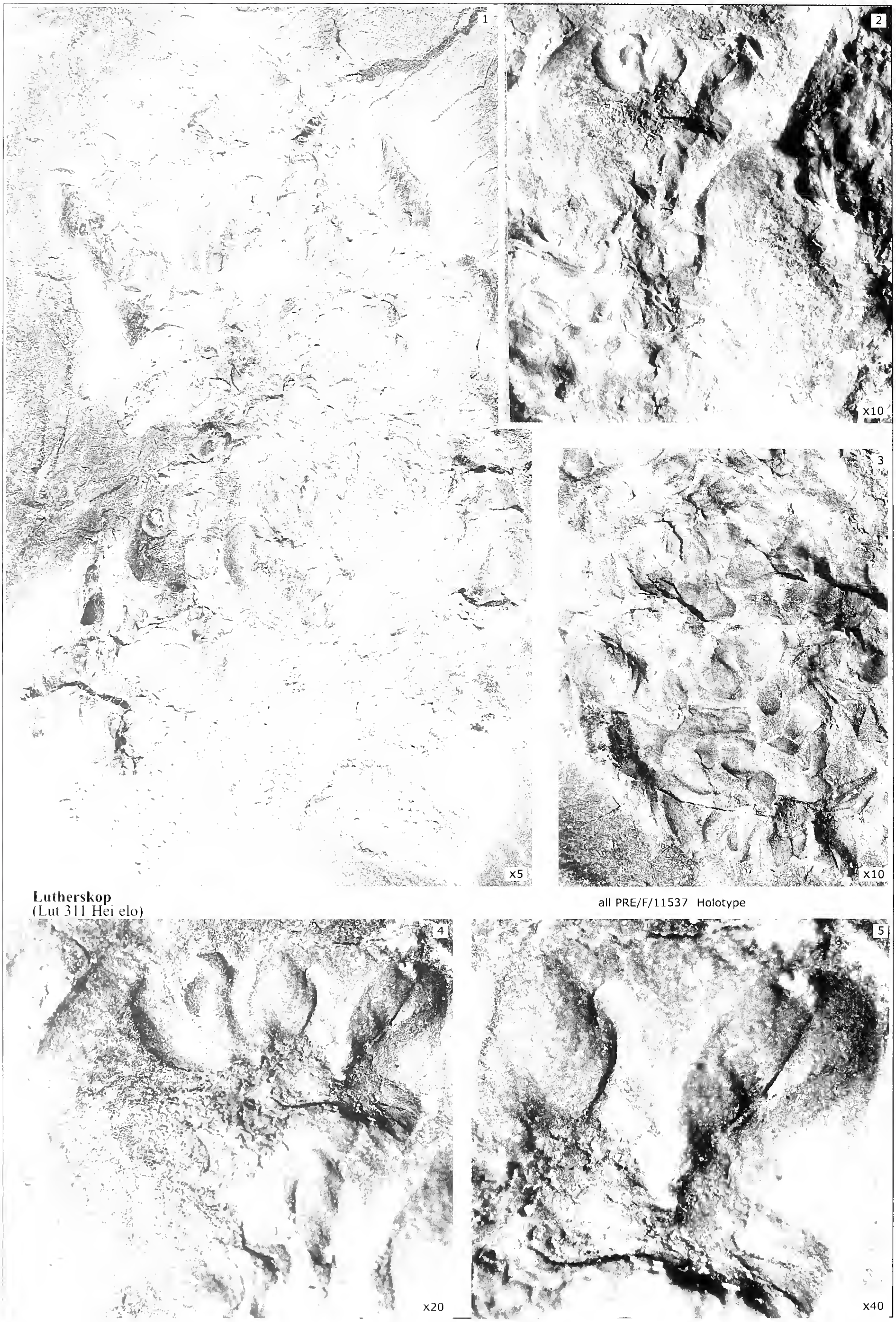
Comment & comparison
L. robustus, based on only one individual from Aas 411, is the least clearly preserved of the three species grouped here under *Lutanthus*, and is, perhaps, the most different. Its particularly stout axis, small microsporophyll laminae, and adaxial clusters of rhomboidal pollen sacs, set it apart. In bearing a single row of microsporangial clusters—though these are adaxial, not abaxial, and with very different sacs—*L. robustus* is reminiscent of *Fredianthus* (pp. 70, 71). The multiribbed scale laminae also show similarities. On these counts, the two taxa could conceivably be congeneric, yet the differences seem more profound than the similarities. The species is placed provisionally under *Lutanthus*, but with obvious reservation.

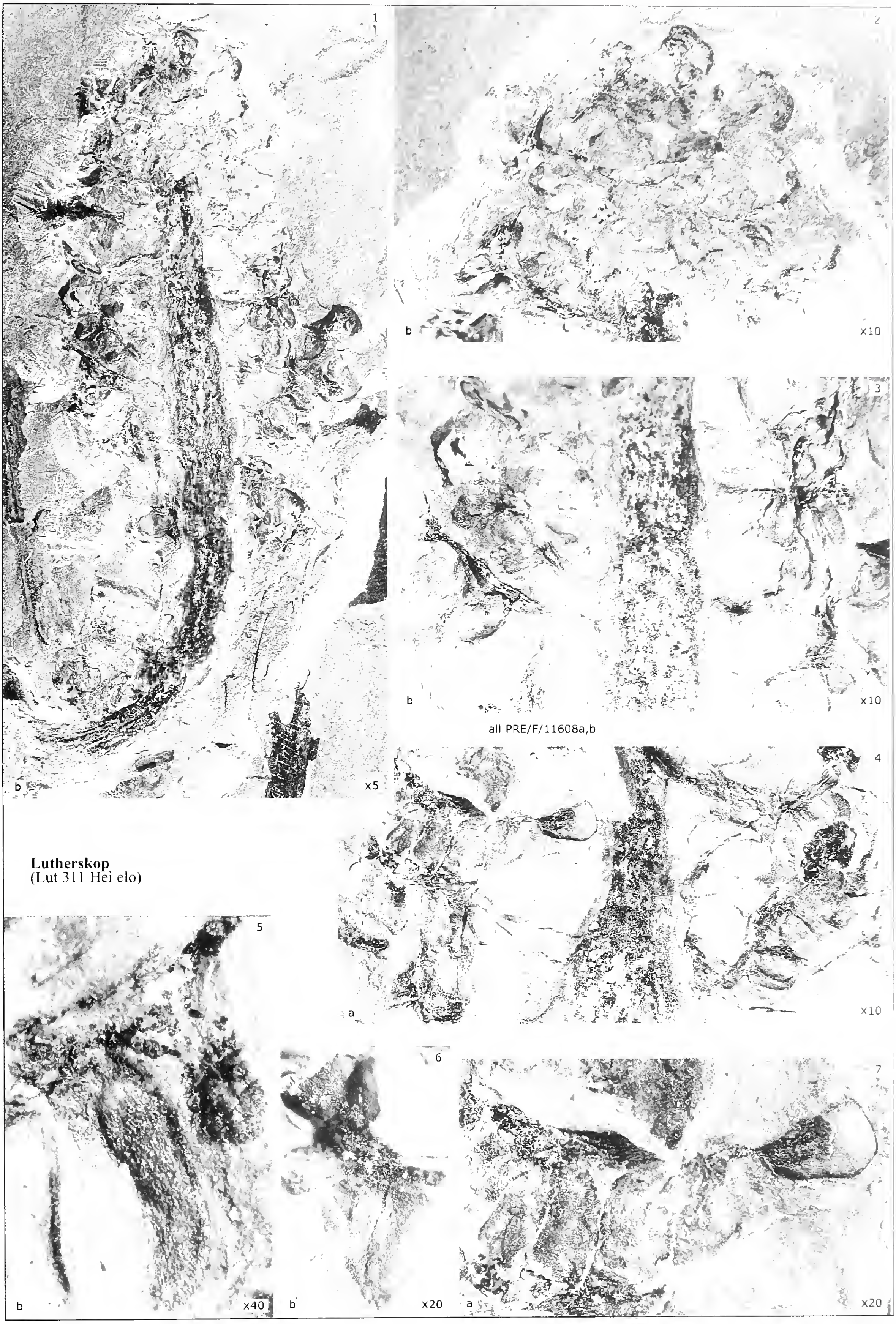


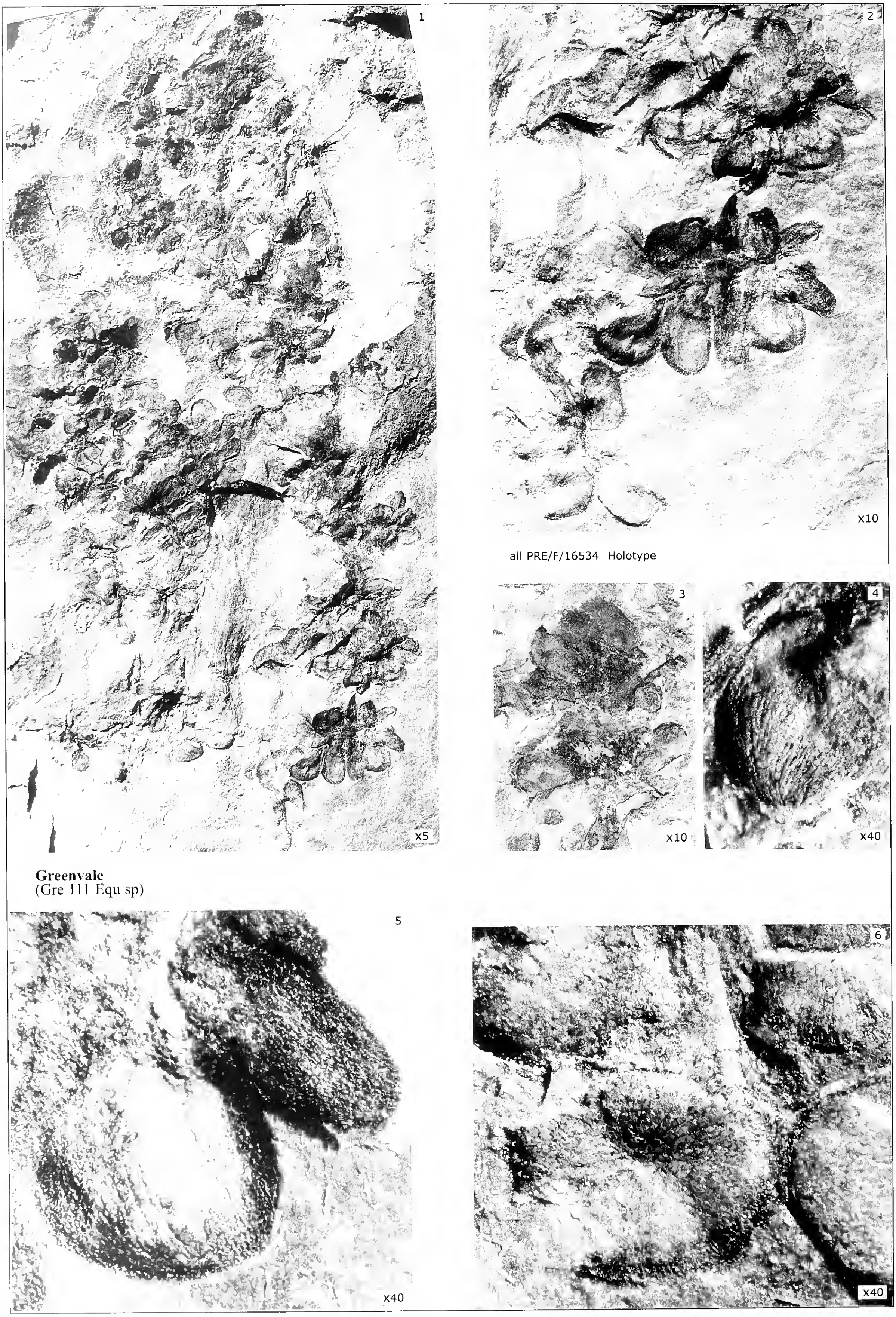







1
2
x10
3
x5
x10
Lutherskop
(Lut 311 Hei elo)
all PRE/F/11537 Holotype
4
5
x20
x40

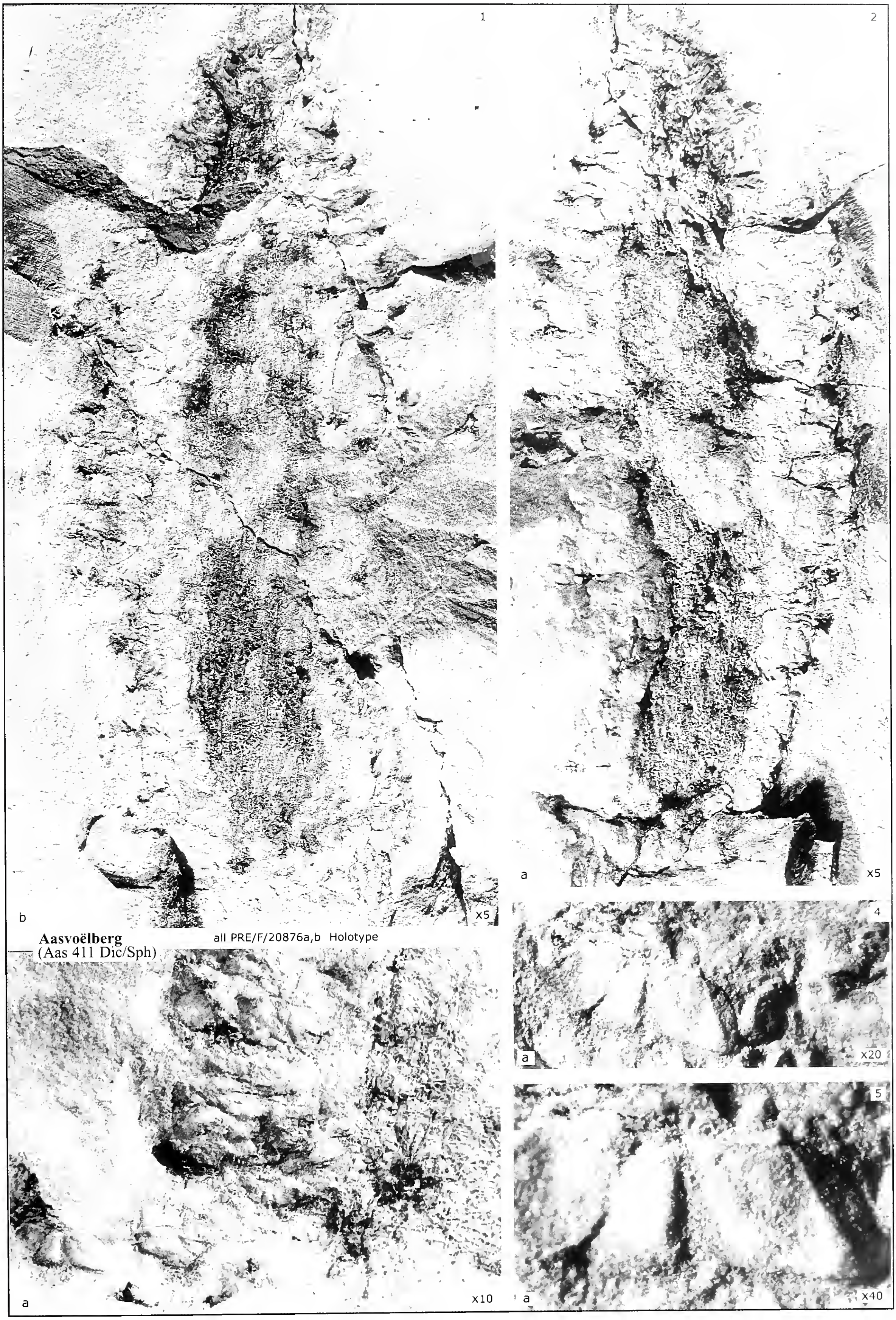

1
b
x5
2
b
x10
3
b
x10
all PRE/F/11608a,b
4
a
x10
Lutherskop
(Lut 311 Hei elo)
5
b
x40
6
b
x20
7
a
x20



all PRE/F/16534 Holotype

Greenvale
(Gre 111 Equ sp)

Lutanthus ornatus **pl. 9** **VOLTZIALES**



VOLTZIALES **pl. 10** *Lutanthus robustus*

PINOPSIDA S.V.Meyen 1984
VOLTZIALES J.M.And. & H.M.And., ord. nov.
VOLTZIACEAE Florin 1951

Telemachus H.M.And. 1978

Type species
Telemachus elongatus H.M.And. 1978.

Generic diagnosis
A voltzialean female cone with megasporophylls bearing a pair of adaxial ovules on a 5-lobed ovuliferous scale.

Generic characters
Attachment: terminal, sessile, erect, occurring singly on woody stem.
Strobilus: simple, compact cone, oval, moderate size (25–75 mm long); axis stout, erect, without free base; megasporophylls helically attached.
Megasporophyll: bract/scale complex extends from axis at right angles; sterile bract fused to ovuliferous scale for half its length, distal end free, leafy (7–45 mm long), often curving strongly to base, linear to lanceolate, proximal margin finely dentate, tapering to acute tip; ovuliferous scale bearing 2 adaxial ovules, distally strongly upturned with 5 distinct acute lobes.
Ovule/seed: naked, oblong to oval (*ca* 4 x 2 mm).

Eponymy
Telemachus—the son of Odysseus and Penelope in Greek mythology; after the holotype locality of the type species.

Global range: 7 spp. Gondwana, Tr. (LAD–CRN).
First: *Telemachus lignosus* (Retallack 1981b); Long Gully Fm., Benmore Dam region, New Zealand.
Last: *Telemachus elongatus* (Anderson 1978); Molteno Fm.

Gondwana Triassic occurrence
SAm—N. Argentina, 2 locs (4 indivs).
SAf —Karoo Basin, 18 TCs (>300 indivs).
Ant —Trans-Antarctic Mts, 2 locs (5 indivs).
Aus —New Zealand, 1 loc. (4 indivs).

Molteno occurrence
Frequency (F): 18 TCs (of 100 sampled in the Molteno).
Diversity (D): 6 species.
Abundance (A): 311 individuals total, abundant (at Gre 121 Hei elo) to very rare (at Pen 321 Dic/Ris).

Qac 111 Hei/Dic:	10	indivs in	4	man-hrs	cleaving	(25	per	1	man-day)	rare
Aas 611 Hei elo:	6	"	" 3	"	"	(20	"	1	")	"
Kle 111 Hei elo:	25	"	" 15	"	"	(20	"	1	")	"
Pen 411 Hei elo:	>50	"	" 70	"	"	(10	"	1	")	"
Kan 112 Hei elo:	10	"	" 15	"	"	(10	"	1	")	"
Tel 111 Hei elo:	40	"	" 90	"	"	(5	"	1	")	"

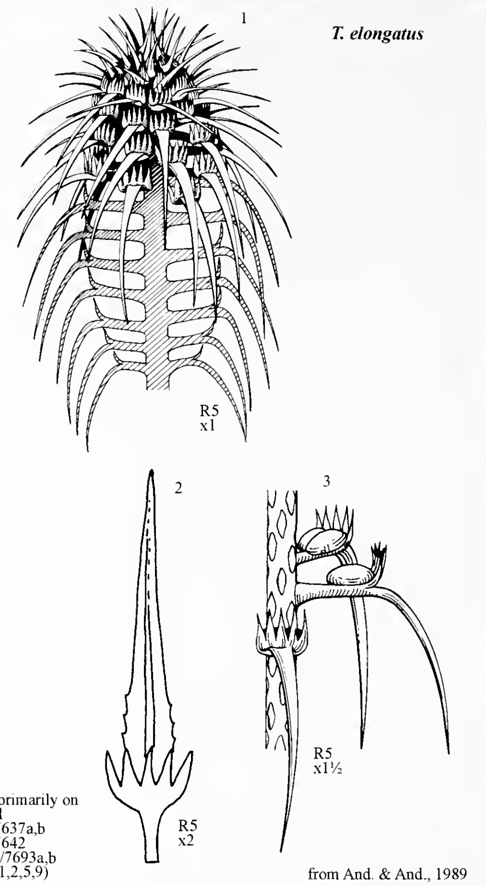
We include data above only for the reference TCs of the six Molteno species described. In that the figures are based exclusively on curated specimens, the relative abundance of *Telemachus* will be generally underplayed. For details of the frequency and abundance of the three affiliated genera, *Telemachus* (female), *Odyssianthus* (male) and *Heidiphyllum* (foliage), through the Molteno, see Tab. 36 (p. 84). For analysis of the mother plant's preferred habitat, and of a typical TC (Aas 311 Hei elo), in which it occurs as a monodominant, see And. & And. (in prep).

Affiliated organs
Male strobilus: *Odyssianthus*—Grade 4 (Kin. reinf., Mut. occ.).
Foliage: *Heidiphyllum*—Grade 4 (Kin. reinf., Mut. occ.).

Evidence for affiliation between the three genera *Telemachus*, *Odyssianthus* and *Heidiphyllum* is convincing both regarding kindred reinforcement and mutual occurrence (see further on pp. 84, 88).

Classification & comparison (see also *Odyssianthus*)
Suprageneric classification (Voltziaceae/Voltziales)
Telemachus and *Heidiphyllum* both fall readily within the morphological ambit of the Voltziaceae as defined in And. & And. (1989, pp. 422, 423). *Podozamites*, a common and widespread Laurasian Late Triassic to Early Jurassic genus, superficially very similar to *Heidiphyllum*, is known in organic connection with the genera *Borysthenia* and *Cycadocarpidium* and in close affiliation with *Swedenborgia*. These three northern genera are typical female strobili of the Voltziaceae.

Intergeneric comparison (Gondwana Triassic)
Telemachus stands as a very clearly defined genus and the only female-cone representative of the Voltziales in the Gondwana Triassic.



based primarily on
Tel 111
BP/2/5637a,b
BP/2/5642
PRE/F/7693a,b
pl. 11(1,2,5,9)
from And. & And., 1989

Reconstructions
The pen sketches (tfs 1–3 above) depicting the type species *T. elongatus* (from Tel 111), with its long, narrowly lanceolate reflexed bracts are Grade 5 reconstructions (R5). They are based on the full reference palaeodeme (pl. 11, figs 1–11) for the species, along with supporting evidence from the sister palaeodeme Aas 111 (pl. 12, figs 10–12).

Bract/scale complex: Two grades of line drawing have been prepared for each species (pp. 85–87): a number of R2 sketches showing the specimens as preserved; and an R4 sketch depicting a complete bract/scale complex representing the norm of the reference palaeodeme.

Molteno occurrence (elaborated)—extracted from And. & And. (in prep.)
Mother-plant (*Heidiphyllum/Telemachus/Odyssianthus*)
The *Heidiphyllum elongatum* mother plant is seen as an erect woody shrub up to 3 m, forming near-monospecific stands in waterlogged habitats.

Foliage (*Heidiphyllum*)
Heidiphyllum, occurring in 62 TCs, is the second most frequent and abundant genus in the Molteno. In the *Heidiphyllum*-thicket TCs it often overwhelmingly dominates the assemblage to the extent where all other taxa together amount to less than 1 or 2% of the total. Where it occurs commonly in TCs of other vegetation types, we visualise the genus as deriving from similar monodominant thickets but of varying extent and varying distance further afield.

Female cone (*Telemachus*)
In strong contrast to *Odyssianthus*, the female, *Telemachus*, either intact or as partial cones or detached scales, is remarkably common. The pattern is clear that this strong presence is almost exclusively associated with the *Heidiphyllum*-thicket TCs. Here it occurs in over half the total number of assemblages.

Male cone (*Odyssianthus*)
The male remains exceptionally rare, with only two cones having been found in a single TC, Telemachus Spruit (Tel 111). Remarkably, these cones are intact, more or less complete, and with *in situ* microsporangia.

Gondwana Triassic occurrence (elaborated)

Although *Heidiphyllum* is one of the most prominent genera (frequency and abundance) throughout the Gondwana Triassic—often a monodominant overwhelming assemblages—its female and male cones (outside of the Molteno) remain extremely rare and absent respectively. A total of only 12 *Telemachus* individuals, all intact strobili, from South America, Antarctica and New Zealand are recorded in the literature (Tab. 35). Remarkably, the cone has not yet been recorded from Australia.

South America (Frenguelli 1942; Spalletti *et al.* 1991)

Frenguelli (1942) described a new genus, *Pterorrachis,* with two species, *P. ambigua* and *P. problematica*, based on two intact cones from a locality near Ischigualasto, San Juan Province, N. Argentina. The photos of the specimens are poor and the reconstruction sketches unconvincing. The material is tentatively identified here as *Telemachus*—an identification supported by the associated occurrence of *Heidiphyllum (Phoenicopsis* in Frenguelli 1942). A distinctive, complete *Telemachus* cone (?species) was found by HMA (22-09-1999) on a field trip (VII International Symposium on Mesozoic Terrestrial Ecosystems) to Ischigualasto—El Gusano locality, Los Rastros Fm. It was given to Alfredo Monetta for their collection at San Juan.

A fourth (possible) cone was recorded and illustrated by Spalletti *et al.* (1991) from Arroyo Lapa, Lapa Fm., Neuquen Basin, central Argentina, and identified as *Telemachus elongatus*. The specimen is intact, but very unclear and not identifiable to species.

Antarctica (Yao *et al.* 1993; Axsmith *et al.* 1998a)

A total of five intact *Telemachus* strobili (compressions) have thus far been recorded from two widely separated localities, Mount Falla and Allan Hills, in the Triassic strata of the Transantarctic Mountains.

The Mount Falla locality (Yao *et al.* 1993) occurs in the Queen Alexandra Range (Buckley Island Quadrangle) within the Lower Falla Fm. of the latest Ladinian. Though intact and clearly preserved, the two Mount Falla specimens do not show the diagnostic bract/scale features and are thus included in the hypodigm table under *T.* spp. indet. Yao *et al.* note that numerous specimens of *Heidiphyllum* are 'found together with *Telemachus* in the Falla Formation'.

The three Alan Hills specimens (Axsmith *et al.* 1998b) from the Lashly Fm. are likewise intact and clearly preserved, yet do not adequately show the diagnostic bract/scale features. In this case, since one of the cones does at least show elongate bract scales, we include the three-specimen palaeodeme tentatively as *T. elongatus.*

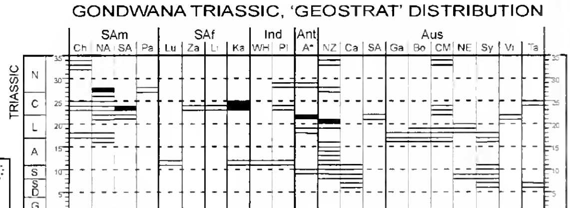
New Zealand (Retallack 1981b)

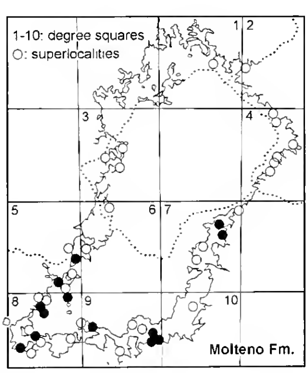
Telemachus lignosus, described by Retallack (1981b) on the basis of four intact cones, derives from cuttings along the Backyards to Otematata River road (S117/f754), Long Gully, Long Gully Fm., Upper Corbies Creek Group, Kaihikuan Stage, Ladinian. The specimens are not clearly preserved, but from the pen sketches and reconstruction of Retallack, the bract/scale complex, with short bracts and scales lacking obvious outer angles (elbows), appears sufficiently different from any of our Molteno taxa to warrant recognition as a distinct species. The low-diversity TC yielding *T. lignosus* includes *Heidiphyllum*, but Retallack does not record relative abundance data.

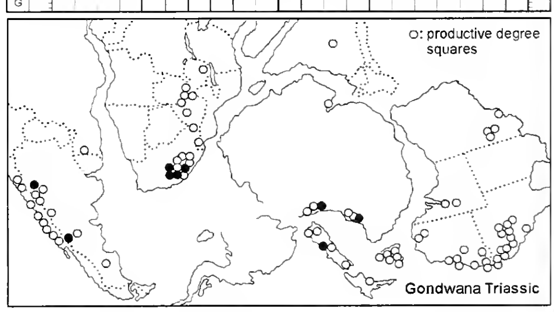
Tab. 35.

***TELEMACHUS* HYPODIGM, Gondwana Triassic occurrence**

AUTHOR	SUBREGION (°square)	FORMATION	LOCALITY	NAME (original)	Indivs ILLUS.	Species: Molteno: T. elongatus	T. grandis	T. serribractus	T. brachybract.	T. dubibractus	T. acutisquamus	Other: T. lignosus	T. spp. indet	Intactness: Intact strobili	Fragmentary "	Isolated scales
SOUTH AMERICA																
1942 Frenguelli	Ischigualasto NA1	? ?	nr. Ischigualasto	*Pterorrachis ambigua*	1 pl 1(1), tf 1	-	-	-	-	-	-	-	1	1	-	-
" "	" "	? ?	" "	" *problematica*	1 pl 1(2,3), tf 2	-	-	-	-	-	-	-	1	1	-	-
1991 Spalletti *et al.*	Paso Flores SA1	24 Lapa Fm.	Arroyo Lapa	*Telemachus elongatus*	1 pl 3(a)	-	-	-	-	-	-	-	1	1	-	-
ANTARCTICA																
1993 Yao *et al.*	Beardmore Glacier TA4	22 L. Falla Fm.	Mount Falla	*Telemachus elongatus*	2 pl 1(1-5)	-	-	-	-	-	-	-	2	2	-	-
1998a Axsmith *et al.*	Allan Nunataks TA1	22 Lashly Fm.	Allan Hills	" "	3 pl on p710(18-20)	3	-	-	-	-	-	-	-	3	-	-
NEW ZEALAND																
1981b Retallack	Benmore Dam NZ4	21 Long Gully	Long Gully	*Telemachus lignosus*	4 pl 11(J-L), tf 5(A-E)	-	-	-	-	-	-	4	-	4	-	-
SOUTH AFRICA																
1978–1999: And. & And. Molteno literature not included in this table																







assemblage (taphocoenosis)		Genera: Heidiphyllum	♀ Telemachus	♂ Odyssianthus	Species: T. elongatus	T. grandis	T. serribractus	T. brachybractus	T. dubibractus	T. acutisquamus	Incertae (no bracts)	Intactness: intact cones	partial cones	1–2 scales	seeds (dispersed)	(in-situ)	Molteno Cycles
Nav 111	Dic odo	**1**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5
Cal 211	Hei elo	**75**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Bir 211	Sph 2spp	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
311	Hei/Sph	**45**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
111	Sph 2spp	**10**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Dor 111	Hei elo	**85**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4/5
Gre 121	Heo elo	**98**	100	-	100	-	-	-	-	-	-	-	90	10	✓✓✓	2	
111	Sph pon	**10**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Boe 111	Lep sto	**7**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
"	Dic/Hei	**42**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
112	Dic cor	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Cyp 111	Dic cra	**24**	5	-	5	-	-	-	-	-	-	-	2	3	✓	-	
111	Hei elo	**100**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Kan 112	Hei elo	**98**	10	-	-	10	-	-	-	-	-	1	1	8	✓✓	1	3
"	Ast spA	**10**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Tel 111	Hei elo	**89**	40	2	40	-	-	-	-	-	-	7	23	10	✓✓	4	
Vin 111	Dic odo	**28**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Ela 111	Dic odo	**7**	1	-	-	-	-	-	-	-	1	-	-	1	✓	-	
Kra 311	Dic odo	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Lut 111	Hei/Dic	**50**	2	-	2	-	-	-	-	-	-	1	-	1	-	-	
511	Hei elo	**80**	1	-	-	-	-	-	-	-	1	1	-	-	-	-	
411	Hei/Dic	**50**	12	-	-	-	-	-	-	-	12	1	4	7	✓✓	1	
311	Hei elo	**99**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Tin 121	Sph 2spp	**4**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
111	Sch sp.	**10**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
131	Hei/Ast	**50**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Kon 223	Dic odo	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2f
211	Hei elo	**95**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
111	Dic odo	**7**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
"	Sch sp	**10**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
"	Hei elo	**84**	2	-	-	-	-	-	-	-	2	-	2	-	✓	-	
Pen 321	Dic/Ris	**1**	1	-	-	-	-	-	-	-	1	-	-	1	-	-	
211	Dic/Equ	**2**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
421	Dic odo	**4**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
431	Dic/Equ	**5**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
311	Hei elo	**75**	17	-	-	-	-	17	-	-	-	-	10	7	✓✓✓	1	
411	Hei elo	**94**	50	-	-	-	-	50	-	-	-	10	30	10	✓✓✓	7	
Kle 111	Equ sp	**1**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
"	Hei elo	**90**	25	-	-	-	25	-	-	-	-	3	5	17	✓✓	2	
"	Hei/Dic	**49**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Kap 111	Dic/Ris	25	5	-	-	-	-	-	-	-	5	-	-	5	✓✓	-	2e
Ela 112	Dic/Hei	**30**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2d
Nuw 211	Dic 2spp	**1**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Win 111	Hei elo	**79**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Qua 111	Dic odo	**20**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2c
Maz 111	Dic cra	**5**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
211	Hei/Dic	**32**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Hla 213	Dic elo	**1**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2b
Umk 111	Dic 2spp	**7**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Inj 211	Dic dub	**10**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
San 111	Dic cra	**5**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Mng 111	Dic 2spp	**6**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Qac 111	Hei/Dic	**50**	10	-	-	-	-	-	10	-	-	3	2	5	✓	-	
Mat 111	Dic dub	**4**	12	-	-	-	12	-	-	-	-	3	7	2	✓	-	
Lit 111	Dic/Hei	**23**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2a
Aas 611	Hei elo	**80**	6	-	-	-	-	-	-	6	-	-	2	4	-	-	1
111	Hei elo	**77**	12	-	12	-	-	-	-	-	-	1	3	8	✓✓✓	-	
211	Hei elo	**100**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
311	Hei elo	**99**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
411	Dic/sph	**1**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
511	Dic elo	**20**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Bam 111	Dic dub	**1**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Total TCs		62	18	1	5	1	2	2	1	1	6	10	13	16	14	7	
Total indivs		%	311	2	159	10	37	67	10	6	22	31	181	99	✓	18	

Tab. 36. *Telemachus*/*Heidiphyllum*, Molteno occurrence

Evidence for affiliations

Foliage: *Heidiphyllum*—Grade 4 reliability

As in the case of four further Molteno female strobili, *Umkomasia*, *Peltaspermum*, *Rissikistrobus* and *Fraxinopsis*, the foliage affiliate of *Telemachus* is almost certainly—short of organic attachment—established. The foliage genus *Heidiphyllum*, abundant and widespread throughout Gondwana during the Middle and Upper Triassic, occurs in close mutual occurrence with *Telemachus* in three, perhaps four, continents in which the latter is now known.

South Africa (Tab. 36)—*Telemachus* is known from 18 of the 100 Molteno TCs sampled. *Heidiphyllum* occurs in all of these TCs, in 14 cases as a co-dominant to dominant element of the assemblage.

South America (Frenguelli 1942)—*Phoenicopsis* (i.e. *Heidiphyllum*) reportedly occurs on the reverse of both fossiliferous slabs bearing possible *Telemachus*.

New Zealand (Retallack 1981b)—The single low-diversity TC yielding the four recorded specimens of *Telemachus* includes the genus *Heidiphyllum*. Retallack does not record the relative abundance of the foliage taxa occurring at the site.

Antarctica (Yao *et al.* 1993)—*Telemachus* is found in association with numerous specimens of *Heidiphyllum* in the Falla Formation.

Cuticular correspondence

The only available cuticular data on *Telemachus* are those of Yao *et al.* (1993), who illustrate and describe a number of fragments from Antarctic material, which they consider well preserved but in our scheme we rate fair (Grade 3).

In our revision of Molteno gymnosperm foliage (And. & And. 1989, pp. 54, 55), *Heidiphyllum* cuticle fared poorly—with only three of the 23 leaves sampled for maceration from Lit 111 and Umk 111 yielding fragments of fair (Grade 3) preservation. Most revealed poor (Grade 2) to very poor (Grade 1) preservation. The best cuticular results obtained from Umk 111 and Lit 111 complement one another, the former based on a macerated specimen, the latter on a relatively transparent cellulose-acetate peel.

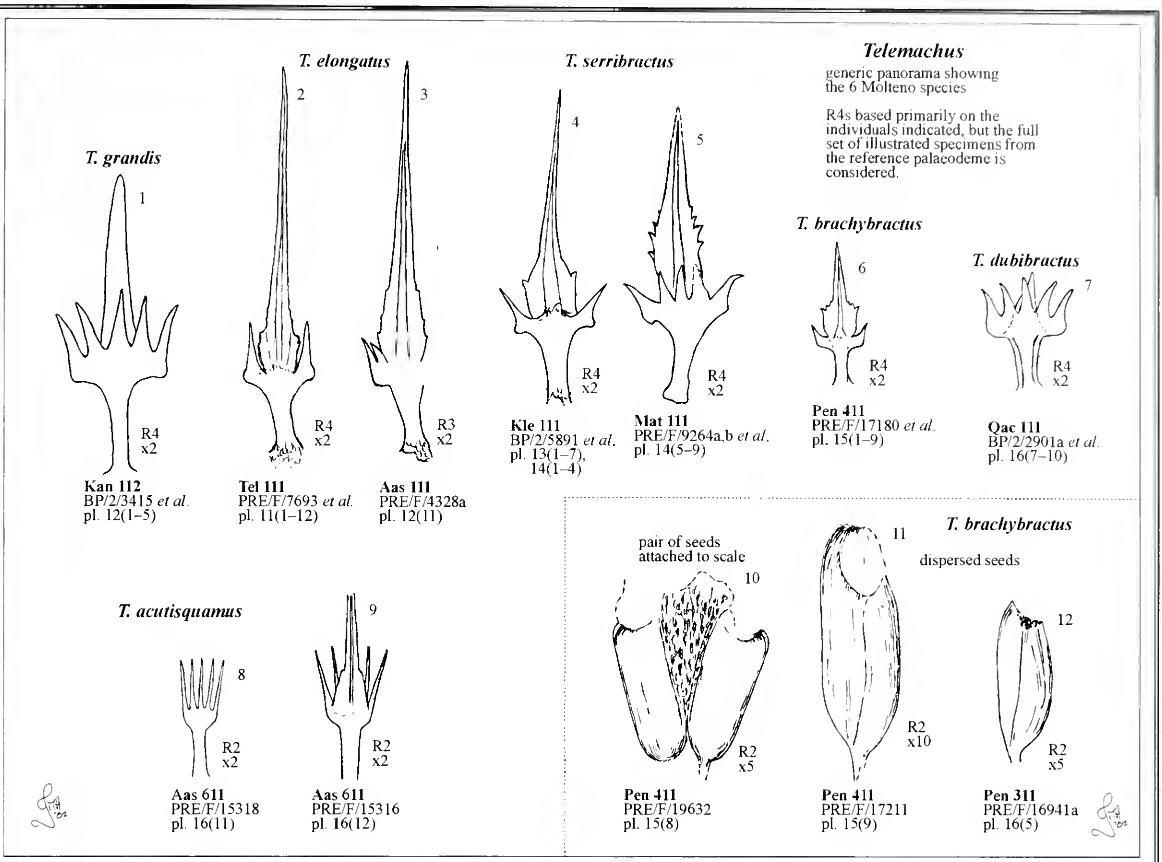
On the basis of the incomplete results at hand, the comparison between the cuticle of *Heidiphyllum* and *Telemachus* is suggestive but inconclusive. The oblong to pentagonal or hexagonal cells with straight to gently curved walls are similar, as are the five or six noncutinised, anomocytic subsidiary cells surrounding the stomata. Strongly cutinised guard-cells appear to be a feature of both taxa, but are not always preserved. The bold papillae of the lower cuticle and the stomatal lappets in *Heidiphyllum* have not been observed in *Telemachus*.

Male strobilus: *Odyssianthus*—Grade 3 reliability

The male counterpart of *Telemachus* is extremely infrequent and rare in the Molteno, being known from only two individuals from 1 TC (Tel 111). *Heidiphyllum* is the overwhelming dominant (89%) in this assemblage.

Kindred reinforcement

Telemachus and *Heidiphyllum* both fall readily within the morphological concept of the family Voltziaceae as delimited and summarised in And. & And. (1989, pp. 422, 423). A generous range of female cone genera are included in the family. *Podozamites*, a common and widespread Laurasian U. Triassic to L. Jurassic foliage genus, superficially very similar to *Heidiphyllum*, is known in organic connection with the genera *Borysthenia* and *Cycadocarpidium* and in close affiliation with *Swedenborgia*. The latter three genera are typical female strobili of the Voltziaceae.



Intactness of cones (Tab. 36)

Degree of cone fragmentation

A substantial proportion of *Telemachus* individuals are found as intact or partially intact cones. While the proportions indicated in the table are inevitably biased towards the more complete material, it is perhaps reasonable to estimate that around 5% of *Telemachus* specimens overall are found as more or less fully intact cones.

In situ *seeds*

Most *Telemachus* cones, partial cones or isolated scales found in the Molteno Fm. have lost their seeds. In only seven of the 18 TCs yielding *Telemachus* do any *in situ* seeds occur; in these seven TCs only a small proportion (10% or less of individuals) still bear any seeds, and in those few cones still bearing seeds, more often than not only a few seeds remain *in situ*. A selection of cones from four TCs (mostly illustrated, pls 11–16) showing different states of seed dispersal are noted below.

Kle 111 Hei elo (8 intact or fragmentary cones)—In this TC a particularly interesting suite of clearly preserved cones occurs—BP/2/5889 is a cone seen in cross-section with most seeds still *in situ*; BP/2/5889 is a longitudinal section of cone with most seeds lost, while BP/2/5891 is a fine cross-section of cone with all seeds lost (pl. 13).

Pen 411 Hei elo (40 intact or fragmentary cones)—This TC has yielded the most comprehensive *Telemachus* palaeodeme as well as numerous readily identified dispersed seeds. PRE/F/19632 (pl. 15(8)) is the clearest specimen in the Molteno collection showing a pair of seeds attached to a scale.

Kan 112 Hei elo (2 intact or fragmentary cones)—PRE/F/20080a,b is the sole instance in the Molteno collection where the cone is found attached—terminally on a short section (2 cm) of stout broken shoot (pl. 12(1–3)). A few seeds remain *in situ* in this specimen.

Lut 411 Hei/Dic (5 intact or fragmentary cones)—PRE/F/14715 is a partial cone with a particularly full complement of *in situ* seeds (not illustrated).

Dispersed seeds

Dispersed seeds are recorded at a further five TCs aside from the four listed above. It should be noted that only those TCs yielding *Telemachus* have been checked for scattered seeds and most of these bear the disseminules in fair numbers.

Adaptive radiation (Molteno diversity)

Telemachus (female strobilus)

As in at least two other notable Molteno plant-genera, *Peltaspermum/Lepidopteris and Fraxinopsis/Yabeiella,* diversification in *Telemachus/Heidiphyllum* is more evident (morphologically manifested) in the female strobilus than in the male counterpart or the foliage. It is in the bract/scale complexes, and in particular the shape, marginal dentition and size of the bracts, that the signature of the six species is best portrayed (tfs 1–9 above). It should be noted that in only six of the 18 *Telemachus*-yielding TCs are the bracts sufficiently preserved to allow the execution of line drawings; and even in these instances, only one or two specimens show a few bracts that are reasonably complete.

The six Molteno species are based on the following TCs and reference palaeodemes. All derive from *Heidiphyllum* thicket, but they are well scattered through the Molteno stratigraphic sequence.

T. elongatus—Tel 111 Hei elo (Telemachus Spruit), 40 indivs
Heidiphyllum thicket; Cycle 3 (Mayaputi Member)
T. grandis—Kan 112 Hei elo (Kannaskop), 10 indivs
Heidiphyllum thicket; Cycle 3 (Mayaputi Member)
T. serribractus—Kle 111 Hei elo (Kleinhoek), 25 indivs
Heidiphyllum thicket; Cycle 2f (Indwe Member)
T. brachybractus—Pen 411 Hei elo (Peninsula), 17 indivs
Heidiphyllum thicket; Cycle 2f (Indwe Member)
T. dubibractus—Qac 111 Hei/Dic (Qachasnek), 10 indivs
Heidiphyllum thicket; Cycle 2c (Indwe Member)
T. acutisquamus—Aas 611 Hei elo (Aasvoëlberg), 6 indivs
Heidiphyllum thicket; Cycle 1 (Bamboesberg Member)

Uncertainty—These six species are recognised by JMA, but with reservation by HMA who feels that there is no bract preserved in the Qac 111 specimens (*T. dubibractus*) and agrees that although the scale lobes appear distinct in the Aas 611 form (*T. acutisquamus*), this could be due to some difference in preservation. Furthermore, HMA does not recognise the bract (as drawn) in the PRE/F/15316 specimen (tf. 9 above) of this Aas 611 palaeodeme.

Telemachus elongatus H.M.And. 1978

Holotype
Specimen: BP/2/5637a,b (C-T.S.326a,b; H.M.And. 1978); pl. 11(1–3).
Assemblage (TC): Tel 111 Hei elo; Telemachus Spruit.
Preservation: virtually complete cone, part and counterpart, longitudinal section; compression with ferruginised woody remains, *ca* 60% flattened; impression in thickly laminated, light olive-grey shale with poor cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 40 indivs (7 intact, 23 partial, 10 detached scales), tfs 1–4 adjacent, pl. 11(1–12).

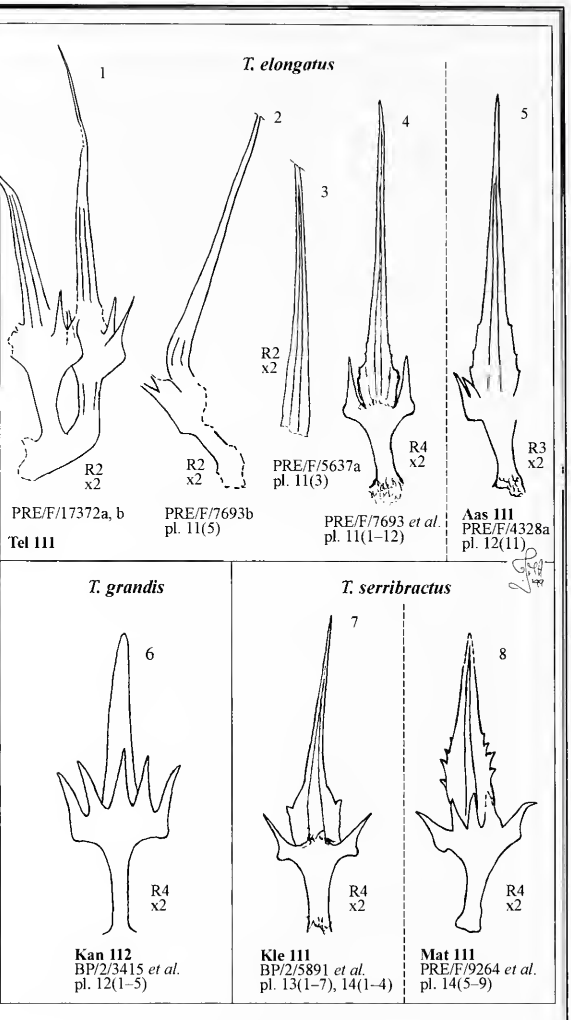
Sister palaeodemes—4 (best 3 listed)
Gre 121 Hei elo: >100 indivs (90 partial).
Aas 111 Hei elo: 12 indivs (1 intact, 3 partial).
Lut 111 Hei/Dic: 2 indivs (1 intact, 1 detached scale).

Specific diagnosis
A *Telemachus* cone bearing long (*ca* 23 mm), narrowly lanceolate, gradually tapering bracts with finely dentate proximal margins.

Specific characters
Strobilus: of intermediate size (50 mm long).
Megasporophyll: bract 23 mm long, narrowly lanceolate, tapering gradually to acute tip, proximal margin finely dentate.

Etymology
elongatus (Lat.)—with reference to the elongate bracts.

Comment & comparison
Identified from five Molteno TCs, this appears to be the most frequently occurring of the *Telemachus* species. It is characterised by the particularly long, finely toothed bracts.



Telemachus grandis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/20080a,b; pl. 12(1–3).
Assemblage (TC): Kan 112 Hei elo; Kannaskop.
Preservation: virtually complete cone attached to stout pedicel, part and counterpart, longitudinal section, with a few *in situ* seeds; impression in very thin-bedded, moderately baked, medium grey shale with poor cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 10 indivs (1 intact, 1 partial, 8 detached scales), tf. 6 adjacent, pl. 12 (1–5).

Sister palaeodemes—nil.

Specific diagnosis
A *Telemachus* cone of particularly large size bearing intermediate-length (*ca* 13 mm) broadly lanceolate bracts without evident dentition along proximal margins.

Specific characters
Strobilus: large (*ca* 70 mm long).
Megasporophylls: bract *ca* 13 mm long, broadly lanceolate, with no apparent marginal dentition.

Etymology
grandis (Lat.)—with reference to the relatively large size of the cones.

Comment & comparison
This species is unique to Kan 112, interpreted as a crevasse-splay deposit. The cone is distinctly larger than in the other Molteno species.

Telemachus serribractus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: BP/2/5891a,b; pl. 13(1–3, 6).
Assemblage (TC): Kle 111 Hei elo; Kleinhoek.
Preservation: complete cross-section of cone, part and counterpart, with a few *in situ* seeds, impression in very thin-bedded, medium light grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 25 indivs (3 intact, 5 partial, 17 detached scales), tf. 7 above, pls 12(1–7), 13(1–4).

Sister palaeodemes—1 only.
Mat 111 Dic dub: 12 indivs (3 intact, 7 partial).

Specific diagnosis
A *Telemachus* cone bearing intermediate-length (*ca* 17 mm) lanceolate bracts with pronounced proximal shoulders and marked dentition.

Specific characters
Strobilus: of intermediate size (*ca* 50 mm long).
Megasporophyll: bract *ca* 17 mm long, lanceolate, tapering relatively abruptly, proximal shoulders pronounced and strongly dentate.

Etymology
serribractus (Lat.)—with reference to the serrate bracts.

Comment & comparison
This species is known from two TCs, Kle 111 and Mat 111. Its recognition, as distinct from *T. elongatus*, seems justified on the basis of the more abruptly tapering, strongly dentate bracts.

Telemachus brachybractus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/18070; pl. 15(1).
Assemblage (TC): Pen 411 Hei elo; Peninsula.
Preservation: half-complete cone, without counterpart; longitudinal section; seeds dehisced; impression in thickly laminated, greenish grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 50 indivs (10 intact, 30 partial, 10 detached scales), tfs 1–3 adjacent, pl. 15(1–9).

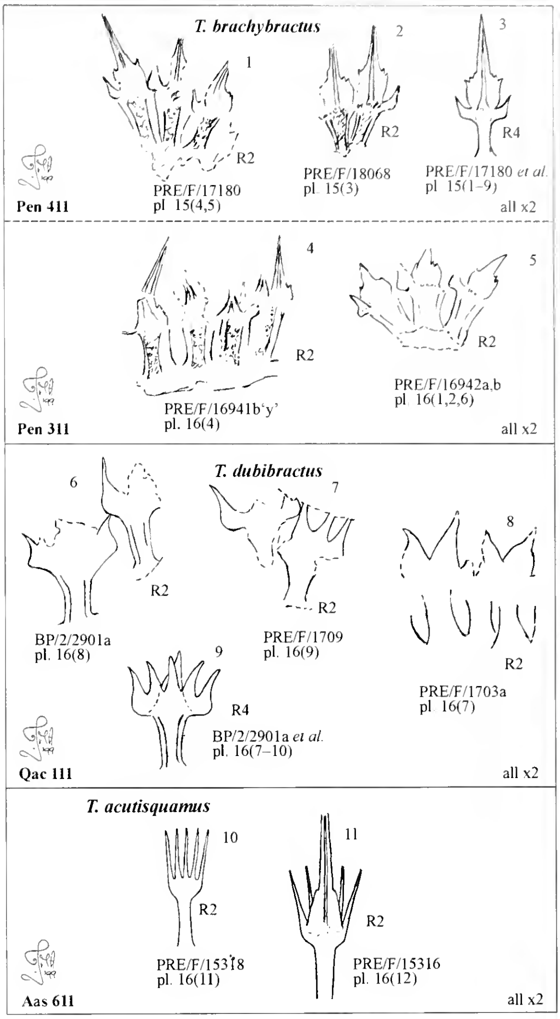
Sister palaeodemes—1 only.
Pen 311 Hei elo: 17 indivs (10 partial).

Specific diagnosis
A *Telemachus* cone of particularly small size bearing short (*ca* 7 mm) lanceolate bracts with strongly pronounced proximal shoulders and marked dentition.

Specific characters
Strobilus: small (25–35 mm long).
Megasporophyll: bract *ca* 7 mm long, lanceolate, tapering fairly abruptly, proximal shoulders pronounced and strongly dentate.

Etymology
brachybractus (Lat.)—with reference to the short bracts.

Comment & comparison
This species is represented by only two palaeodemes from TCs (*Heidiphyllum* thicket of the floodplain) occurring within the same intermittently outcropping mudstone horizon (50–250 mm thick) some 2 km apart along an unpaved road. The cones, of which there are a good number of intact specimens, are consistently smaller than in the other five Molteno species. The small, stout scales are quite distinctive.



Telemachus dubibractus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/1703a,b; pl. 16(7).
Assemblage (TC): Qac 111 Hei/Dic; Quachasnek.
Preservation: intact cone (proximal third missing off edge of slab), with part and counterpart; longitudinal section; seeds apparently shed; impression in thinly laminated, medium light grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 10 indivs (3 intact, 2 partial, 5 detached scales), tfs 6–9 adjacent, pl. 16(7–10).

Sister palaeodemes—nil.

Specific diagnosis
A *Telemachus* cone (apparently) bearing very short (*ca* 4 mm) conical bracts without proximal shoulders or serrations.

Specific characters
Strobilus: of intermediate size (? *ca* 50 mm long).
Megasporophyll: bract *ca* 4 mm long, conical, apparently without proximal shoulders or serrations.

Etymology
dubibractus (Lat.)—with reference to the dubious nature of the bracts.

Comment & comparison
T. dubibractus is unique to Qac 111. This species is provisionally differentiated on the basis of the short bract which is not readily distinguished from the scale lobes. It is assumed (uncertainly) that the bracts are preserved intact (have not been dehisced) in the type specimen—as is the condition of preservation in the many more or less complete cones representing the other Molteno species.

Telemachus acutisquamus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/15318a,b, pl. 16(11).
Assemblage (TC): Aas 611 Hei elo; Aasvoëlberg.
Preservation: partial cone bearing 6 scales, with part and counterpart; seeds shed; impression in medium-bedded, strongly baked, dusky yellow mudstone with poor cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 6 indivs (2 partial, 4 detached scales), tfs 10, 11 above, pl. 16(11, 12).

Sister palaeodemes—nil.

Specific diagnosis
A *Telemachus* cone bearing particularly distinctive scales with gracile, acutely linear lobes, and with intermediate-length lanceolate bracts of uncertain proximal character.

Specific characters
Strobilus: unknown.
Megasporophyll: scale lobes gracile, acutely linear; bract *ca* 9 mm long, shape and margin uncertain.

Etymology
acutisquamus (Lat.)—with reference to the needle-shaped scales.

Comment & comparison
T. acutisquamus is unique to Aas 611. The remarkably needle-like scale lobes are very unlike those in the other five Molteno species.

Odyssianthus J.M.And. & H.M.And., gen. nov.

Type species
Odyssianthus crenulatus J.M.And. & H.M.And., sp. nov.

Generic diagnosis
A voltzialean male cone of medium size (*ca* 70 mm long), with strongly upcurving microsporophylls bearing 2 rows of *ca* 4 latero-abaxial clusters (2–3 sacs each) of microsporangia.

Generic characters
Strobilus: a compact cone, lanceolate, relatively large (70 mm long); axis stout (*ca* 6 mm in diam.), strongly flexed towards base; microsporophylls helically attached, in *ca* 23 gyres of *ca* 16–20 units.
Microsporophyll: a simple scale, proportionately intermediate, strongly upward-curving; distal lamina broadly ovate, margin finely crenulate, with moderate heel; stalk broad, tapering proximally, winged and keeled; microsporangia relatively numerous (*ca* 22–24), latero-abaxial in two rows of *ca* 4 pendent clusters, each with 2 or 3 sessile pollen sacs.
Microsporangium: irregularly rhomboidal (*ca* 1 mm long), with clear longitudinal line (dehiscence slit?) and apical 'micropyle'.
Pollen: unknown.

Eponymy
Odyssianthus—Greek mythology; for Odysseus, the Greek hero at the siege of Troy and father of Telemachus (the name given to the affiliated female cone).

Global range: 1 sp., Gondwana, Tr. (CRN).
First & last: the single Molteno species described here.

Gondwana Triassic occurrence
SAf—Karoo Basin, 1 TC (2 indivs).

Molteno occurrence
Frequency (F): 1 TC.
Diversity (D): 1 species.
Abundance (A): 2 individuals total.

Tel 111: 2 indivs in 90 man-hrs cleaving (1 per 5 man-days) extremely rare

The extreme rarity of the male cone is remarkable considering the frequency and abundance of the affiliated foliage *Heidiphyllum* and the widespread occurrence of the female cone *Telemachus* (see pp. 82, 83).

Affiliated organs
Female strobilus: *Telemachus*—Grade 4 (Kin. reinf., Mut. occ.).
Foliage: *Heidiphyllum*—Grade 4 (Kin. reinf., Mut. occ.).

The affiliation of *Odyssianthus* with the ovulate cone *Telemachus* and the foliage genus *Heidiphyllum* is considered sure (Grade 4 reliability) for reasons of co-occurrence and morphological similarity.

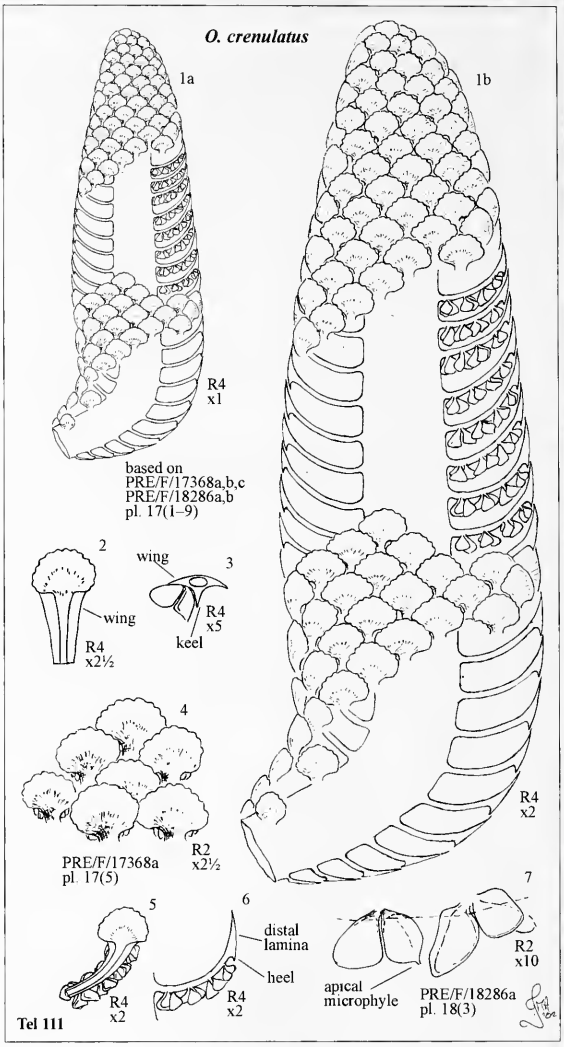
Classification & comparison
Suprageneric classification (Voltziaceae/Voltziales)

Odyssianthus, in view of its Grade 4 affiliation with *Telemachus* (female cone) and *Heidiphyllum* (foliage), rather than its morphology, is included in the Voltziaceae. *Telemachus* (And. & And. 1989, pp. 420–423; this vol., p. 82), in particular, is a typical member of the family.

Morphologically, with its winged scale and double row of *latero-abaxial* microsporangia, *Odyssianthus* is very distinct from the Laurasian genera—*Sertostrobus*, *Darneya* and *Willsiostrobus*, best known from the lower Middle Triassic Gres-a-*Voltzia* Sandstone of France (Grauvogel-Stamm 1978)—that are generally included in the family (this vol., pp. 57, 59). Considering a possible phylogeny based exclusively on male cones (Tab. 31, p. 57), *Odyssianthus* (plus *Lutanthus*) could quite readily be derived from the Permian glossopterid genus *Lidgettonia*. This option would place *Odyssianthus* well distant from the Voltziales, in a new gymnospermous order and would seemingly negate affiliation with *Telemachus*.

Intergeneric comparison (Molteno genera)

While *Lutanthus* and *Fredianthus* are included, possibly conservatively, along with *Odyssianthus* in the Voltziales (an order transitional between the Cordaitanthales and Pinales), they might well be shown, once their ovulate and foliage affiliates are known, to represent different lineages at order level.



Reconstruction
The two available specimens of *Odyssianthus* are excellently preserved, clearly showing both the outer aspect of the cone and longitudinal sections revealing the characteristics of the scales and microsporangial clusters. Even so, the precise number of microsporangial groups and microsporangia per group is not as certain. The base, also, is not clear, but it appears that the cone, as in *Lutanthus*, is sessile (without a free axis).

Adaptive radiation (Molteno diversity)
With *Odyssianthus* sampled from only the single site, it is unknown how morphologically varied or conservative the male cone of this plant-genus might have been with respect to the female cone (*Telemachus*) or foliage (*Heidiphyllum*). Would the pollen cones, as in the case of *Rissikianthus* (pp. 108–111), reflect the same level of species diversity for the genus as the ovulate cones do? The possibility does exist, though we find this unlikely, that either or both of the male cone genera, *Fredianthus* and *Lutanthus* (pp. 70, 71, 74–77), might be congeneric with *Odyssianthus*. If so, the diversity shown by the male cones of the *Telemachus*/*Heidiphyllum* plant-genus would be particularly unusual.

Affiliated organs (elaborated)
Mutual occurrence: As with the other voltzialean male cones from the Molteno, *Odyssianthus* remains extremely rare. It is known only from the two intact specimens from Telemachus Spruit (Tel 111), where *Heidiphyllum* occurs as a monodominant (89% of the foliage in the assemblage) and *Telemachus* is relatively numerous (40 specimens). No other coniferous remains, either foliage or cone, are known from this Tel 111 TC.

Morphological correspondence: In both size and texture *Odyssianthus* and *Telemachus* are very alike, but the one is clearly microsporangiate and the other ovulate.

Odyssianthus crenulatus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/17368a,b; pl. 17(1–7).
Assemblage (TC): Tel 111 Hei elo; Telemachus Spruit.
Preservation: almost complete intact cone (free axis missing), part and counterpart, longitudinal section and outer view, showing numerous scales and *in situ* microsporangia; impression in thickly laminated, light olive-grey shale with poor cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 2 individuals, including the holotype and a second fairly complete cone (PRE/F/18286a,b; pls 17(8, 9), 18(1–7).

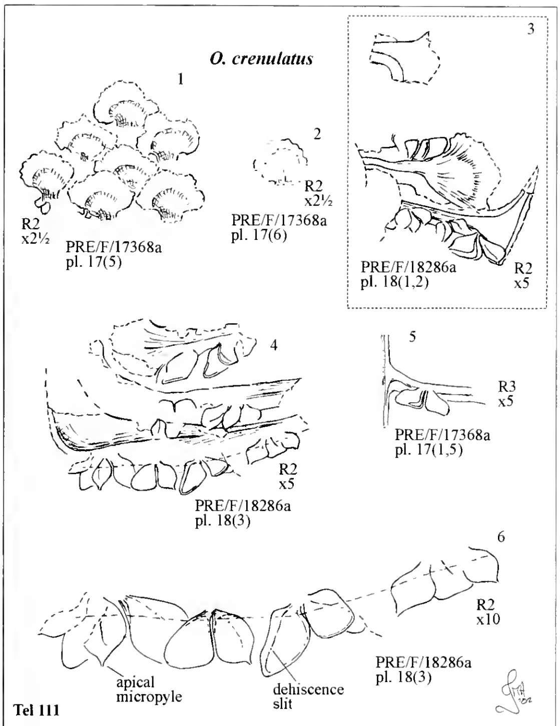
Sister palaeodemes—nil.

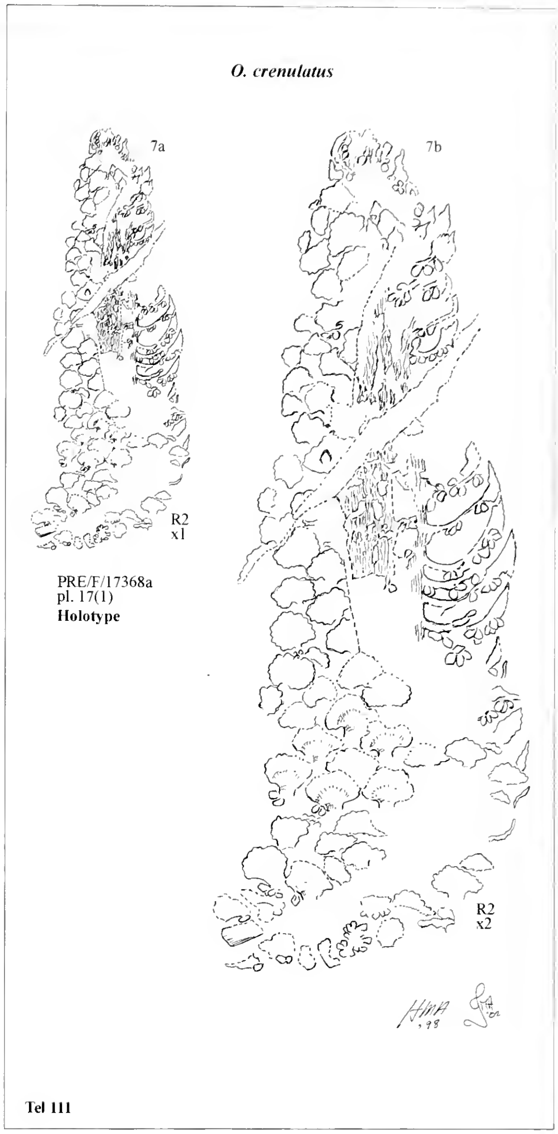
Specific diagnosis—as for genus.

Specific characters—as for genus.

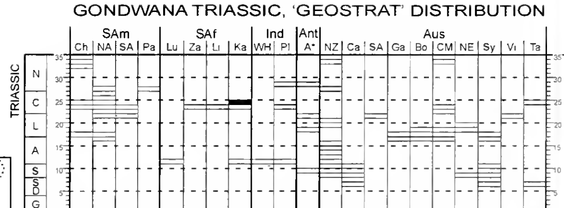
Etymology
crenulatus (Lat.)—with reference to the crenulate nature of the scale margin.

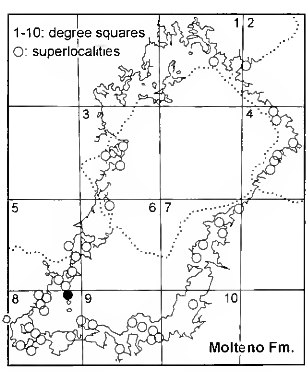
Comment & comparison—see notes for genus.

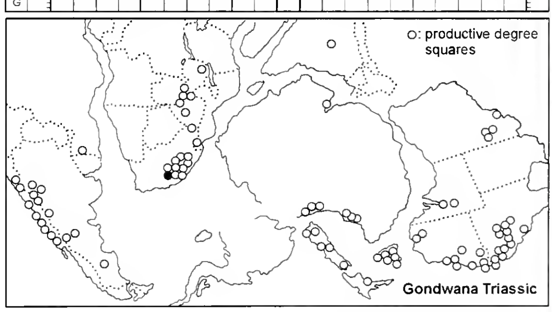




GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION







Heidiphyllum Retallack 1981b

Type species
Heidiphyllum elongatum (Morris 1845) Retallack 1981b.
'Jerusalem Basin', Tasmania; U. Triassic.

Generic diagnosis
A voltzialean leaf of relatively large size, with *ca* 10 parallel veins, attached to short shoots in tight pseudowhorls with short triangular bracts.

Generic characters
Attachment: leaves in tight pseudowhorls on short shoots, in axils of persistent triangular bracts.
Leaf: individually dehisced, relatively large (*ca* 120 x 10 mm), blade broad, flattened, simple, linear to narrowly elliptic or oblanceolate, apex rounded, base narrowly to broadly sessile; veins parallel, moderately spaced (*ca* 10 per 10 mm), forking nearer base, coalescing towards apex.

Cuticle (adapted from And. & And. 1989, p. 429); this vol., tfs 4–6 below.
Yield: Lit 111: 13 specimens sampled; grade index 0/11/2/0/0.
Umk 111: 19 specimens sampled; grade index 1/7/1/0/0.
Diagnostic characters: based on *H. elongatum* (Umk 111).
Adaxial/abaxial: dorsiventral, U & L cuticle of equal thickness.
Cell characteristics: walls straight to gently curved, profile triangular, plan normal; upper cuticle with isodiametric to oblong cells, end walls square to oblique, 350 cells per 1 mm^2, nonpapillate; lower cuticle with pentagonal to hexagonal cells, 600 cells per 1 mm^2, papillae large, bold, usually 2 per cell.
Stomatal apparatus: haplocheilic, ?amphistomatic; subsidiary cells anomocytic, 5 or 6 cells, noncutinised, radial walls normal; Florin ring lappetate, interfingering baculae; (frequency, arrangement, guard cells and stomatal pit unknown).
Other features: none preserved.

Eponymy
Heidiphyllum—named by Retallack (1981b) after Heidi M. Anderson who first described the affiliated cones (Anderson 1978).

Global range: 3 spp., Gondwana, Tr. (ANI–NOR).
First: *H. elongatum* (*Desmiophyllum* sp.) (Lele, 1962b); Beli, S. Rewa, India.
Last: *H. elongatum* (Retallack 1985); Wairoa Gorge, Nelson Syncl., N.Z.

Gondwana Triassic occurrence
Frequency (F): 26 degree squares (of 84 across Gondwana).
Ubiquity (U): 5 continents (of 5 comprising Gondwana).
Diversity (D): 3 foliage species.
Abundance (A): 95% (a monodominant in Molteno TCs).
Longevity (L): 18 myrs (late Anisian to late Norian).

Colonisation success: FUDAL rating 26/5/3/95/18 = 147.
High success (Grade 2): *Heidiphyllum* is the second most prominent genus in the Gondwana Triassic; it was frequent, ubiquitous, abundant and long-lived, but markedly lacking in diversity.
Endemism: of the three Gondwana Triassic species, one is a basin endemic, one a continent endemic, while the third (*H. elongatum*) occurs very widespread throughout the realm.

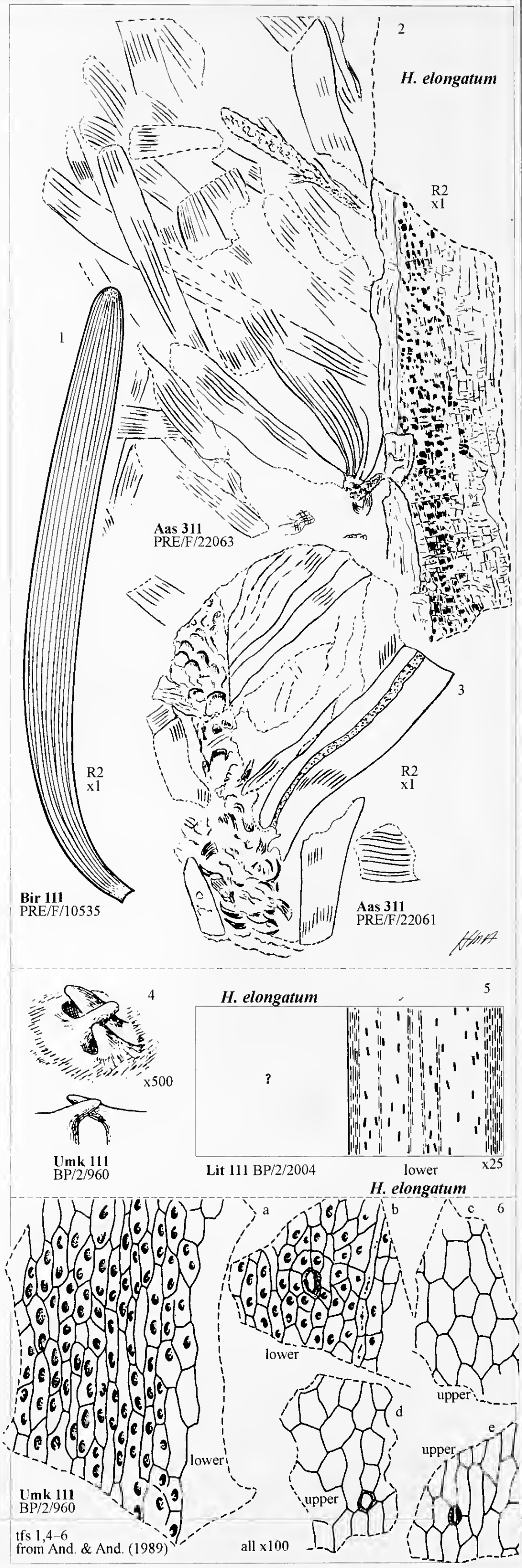
Molteno occurrence
Frequency (F): 62 TCs (of 100 sampled in the Molteno).
Diversity (D): 1 species.
Abundance (A): monodominant (>70%) in its preferred habitat at 19 TCs; co-dominant (20–69%) at 14 TCs; occasional to abundant (1–19%) at 24 TCs; <1% at only 5 TCs.

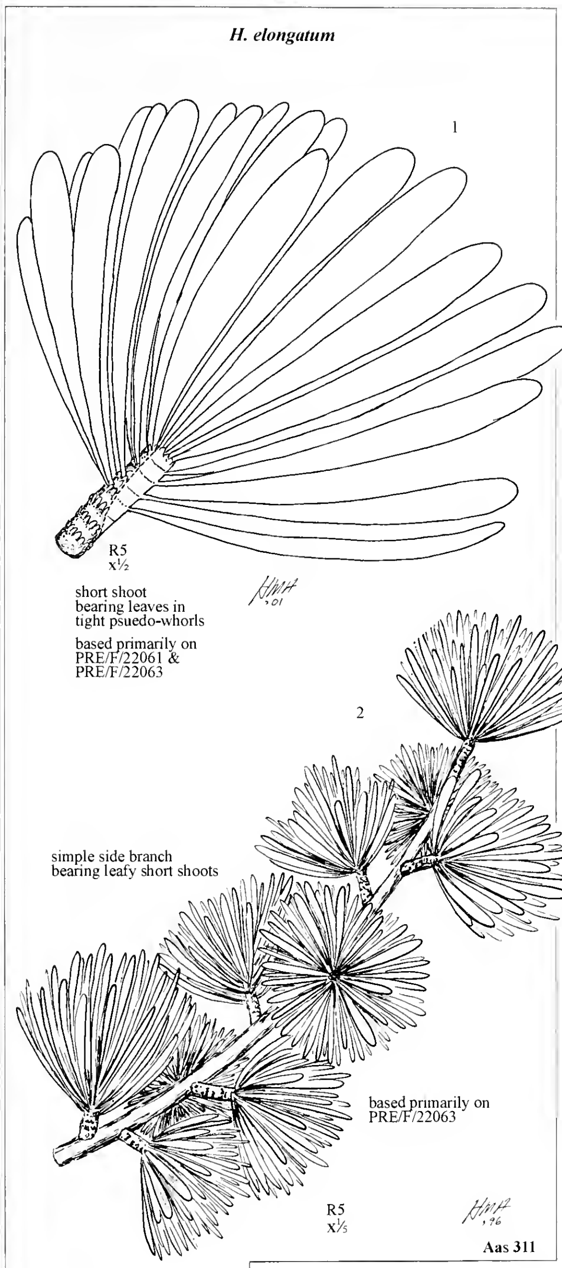
Habit: probably a woody, reed-like plant.
Preferred habitat: *Heidiphyllum* is monodominant in areas of high water table in the floodplain or on channel sandbars.

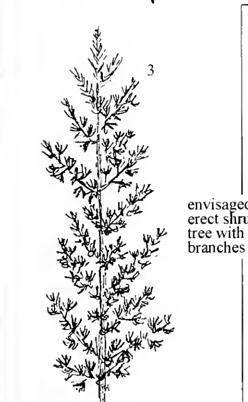
Affiliated organs
Female strobilus: *Telemachus*—Grade 4 (Kin. reinf., Mut. occ.).
Male strobilus: *Odyssianthus*—Grade 4 (Kin. Reinf., Mut. occ.).

Classification & comparison
Gondwana Triassic: Axsmith *et al.* (1998b) describe *Notophyton krauselii*, a permineralised leaf from the Triassic of Antarctica, and consider it as possibly conspecific with *H. elongatum*. They record the leaves as being attached either helically or bijugately (opposite), which would make them more similar to *Clariphyllum*. They find their material to have a possible link to the Podocarpaceae.

Other attached leaves are recorded by Zhou & Zhang (1998) for *Phoenicopsis euthyphylla* from the Middle Jurassic Yima Fm., China. These are attached to short shoots which are in turn attached to a long shoot. Associated with these leaves is *Tianshia patens* (similar to *Clariphyllum*), a leafy shoot with helically arranged leaves, which the authors suggest belongs to the same plant as *P. euthyphylla*.







Reconstructions

The reconstruction of the leaves (tfs 1, 2 adjacent) in pseudowhorls on short shoots attached to an axis is based on a series of specimens from Aas 311: PRE/F/22063 (tf. 2 opposite) shows an axis bearing a small short shoot with leaves attached, probably in a whorl (on this specimen more short shoots and leaves occur but not so clearly); PRE/F/22061 (tf. 3 opposite) and PRE/F/22066 show leaves attached to axes with remains of leaf bases and triangular bracts; PRE/F/11894 shows attached triangular scales. We have used the extant conifer *Pseudolarix amabilis* from China as an analogue. In this taxon the leaves are deciduous and borne on short shoots in a tight spiral. Another extant tree with leaves (in this case evergreen) on short shoots in such a tight spiral that they look whorled is *Sciadopitys verticillata* from Japan.

The occurrence of short shoots and fairly wide stems points to *Heidiphyllum* being woody and not herbaceous like *Aetophyllum* discussed below. Whether *Heidiphyllum* leaves were deciduous or evergreen is unknown, but we regard them as having probably been evergreen.

Literature (supporting evidence & viewpoints)

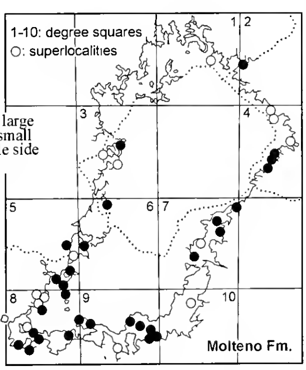
Retallack (1977)—Australia, Clarence-Moreton Basin, Nymboida Colliery, Middle Triassic (Ladinian); *Heidiphyllum* found as a very dominant leaf in the lower part of crevasse splay sandstones, suggesting that it formed a 'levee and point bar scrub or woodland whose leaf litter was scoured out during floods'.

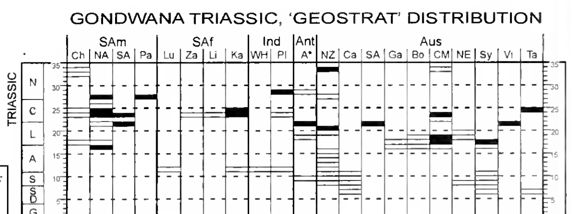
Grauvogel-Stamm (1978)—France, Vosges, Grés a *Voltzia*, Buntsandstein, late Lower Triassic (Spathian); *Aetophyllum*, from the Vosges, must be the most completely known genus within the Voltziales. The material includes: 10 seedlings (five nearly complete) with roots, young stems and leaves; mature plants (one complete male, six nearly complete) with either female or male cones found attached, suggesting plants of 2 m height. All specimens are found near the base of fossiliferous lenses, and judged to be preserved close to their position of growth. Since only a small amount of wood—i.e. secondary xylem—is found in the stems studied, *Aetophyllum* is considered by Grauvogel-Stamm to be herbaceous, a condition previously unknown amongst the Pinopsida. The interpretation is supported by Rothwell *et al.* (2000).

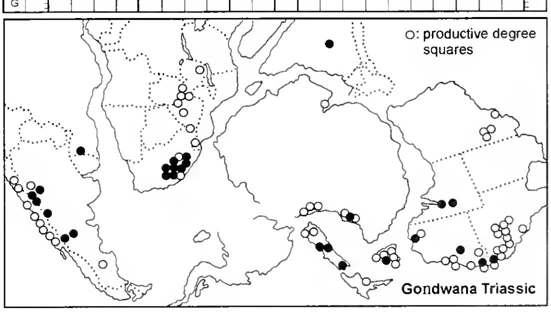
Meyer-Berthaud & Taylor (1991)—Antarctica, Fremouw Fm., Silicified peat locality, Fremouw Peak.

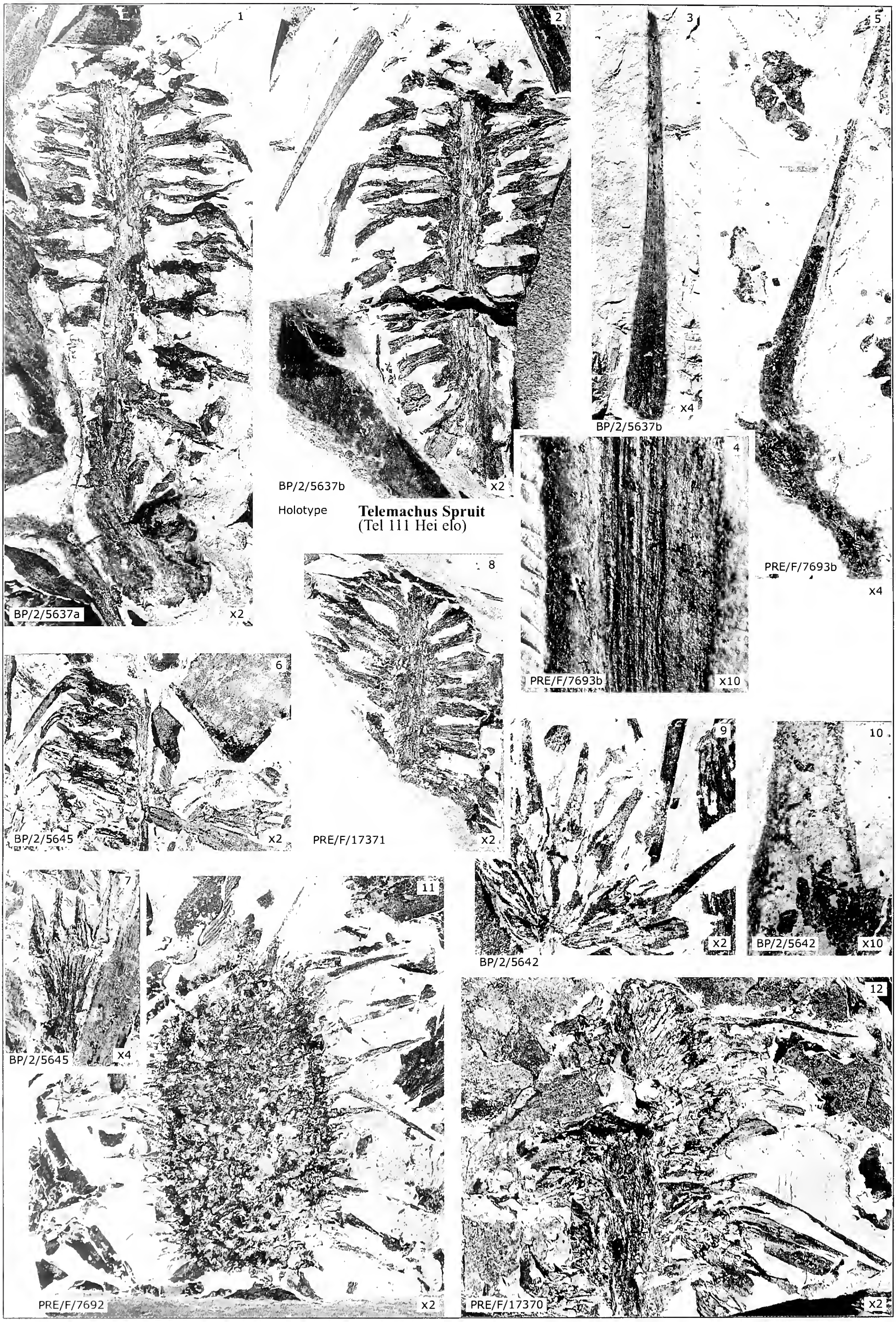
Adaptive radiation (Molteno diversity)

Though *Heidiphyllum* is frequent, occurring in 62 TCs (Tab. 44) and abundant (often monodominant), it is morphologically particularly conservative. Only one apparent species of foliage can be recognised in this great mass of material from the Molteno. The distinct species from Umk 111, previously recognised by us as a species of *Heidiphyllum*, is here placed in the new genus *Clariphyllum* (pp. 100, 101). Two additional species are recognised (And. & And. 1989) in collections from Gondwana deposits further afield.

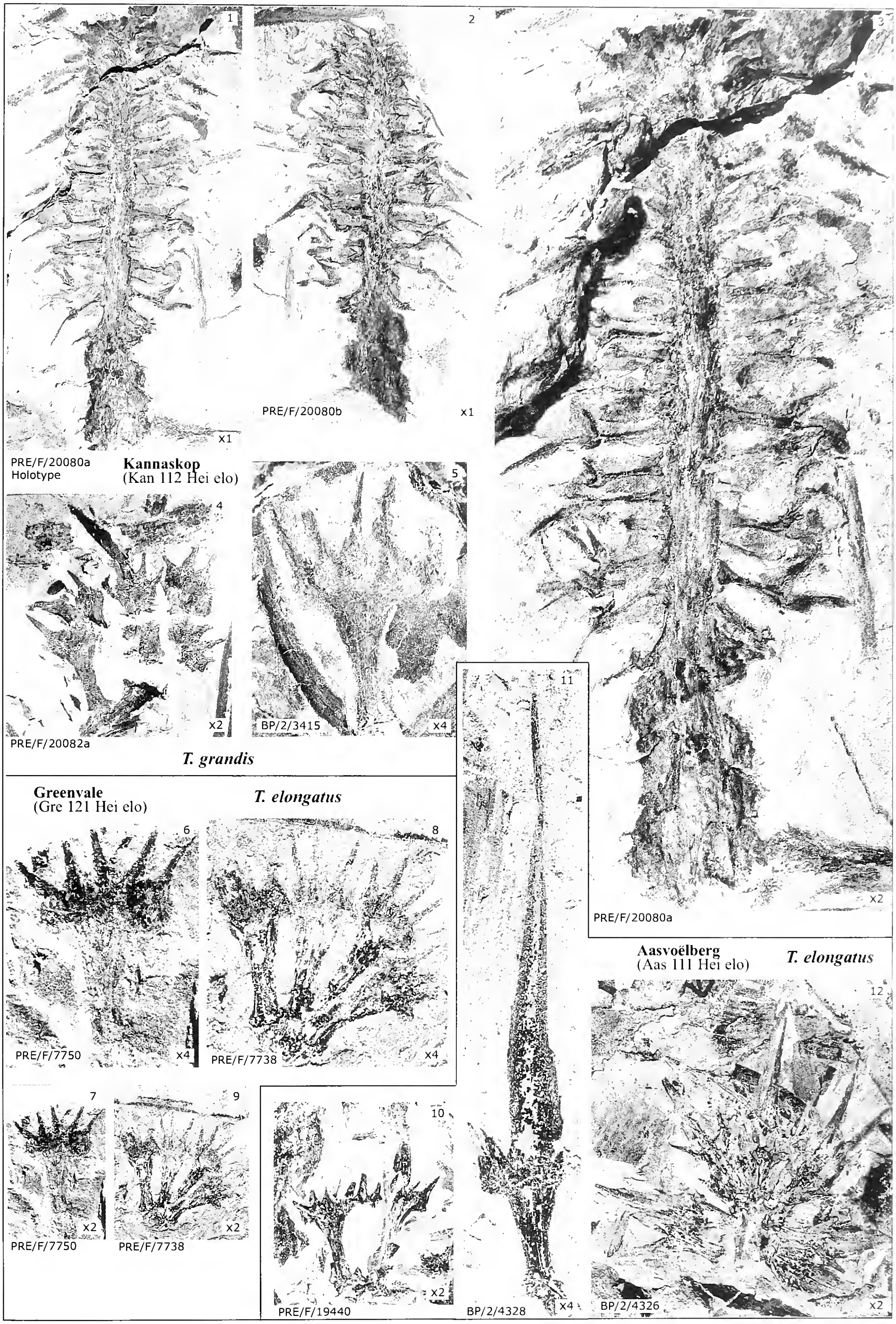


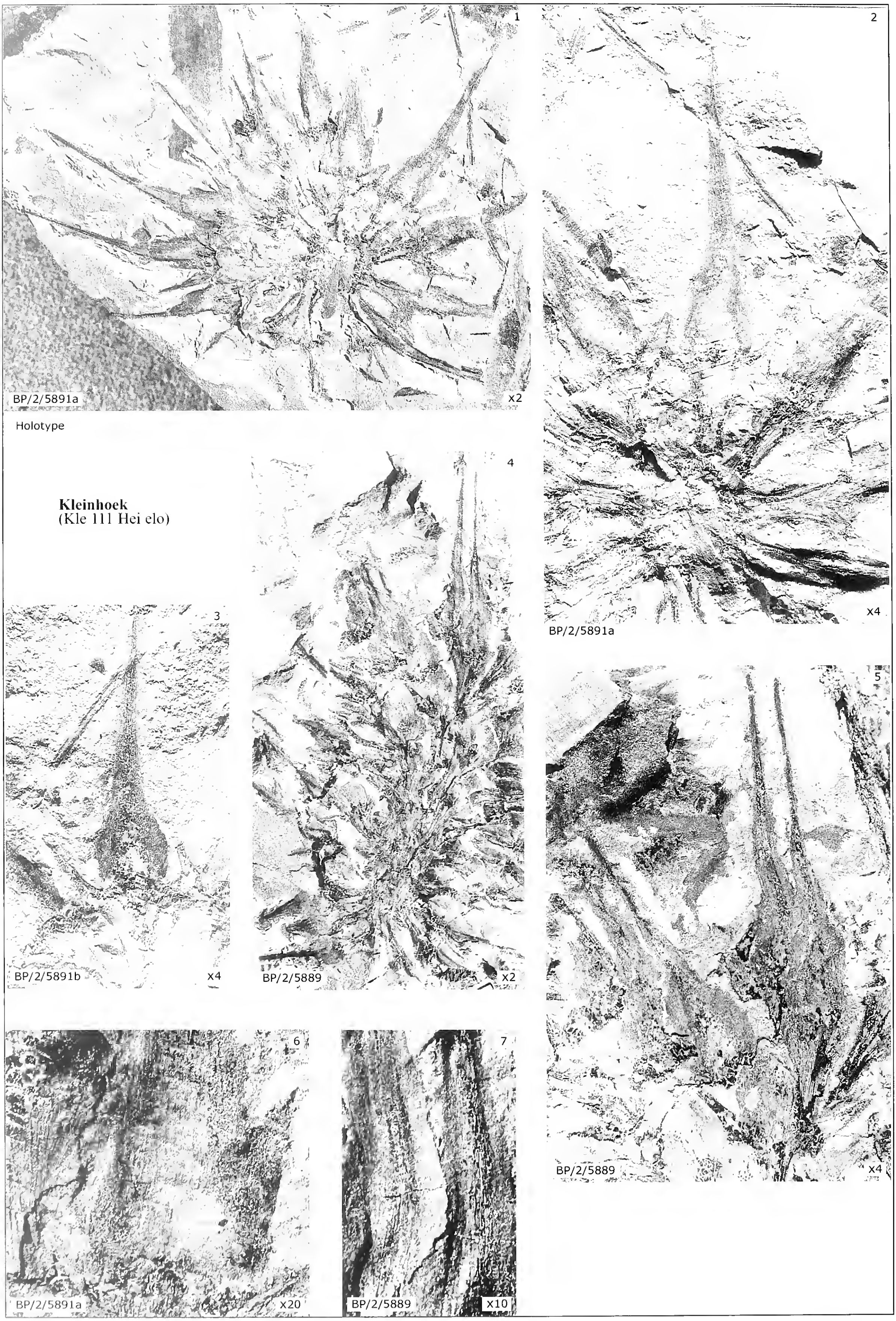




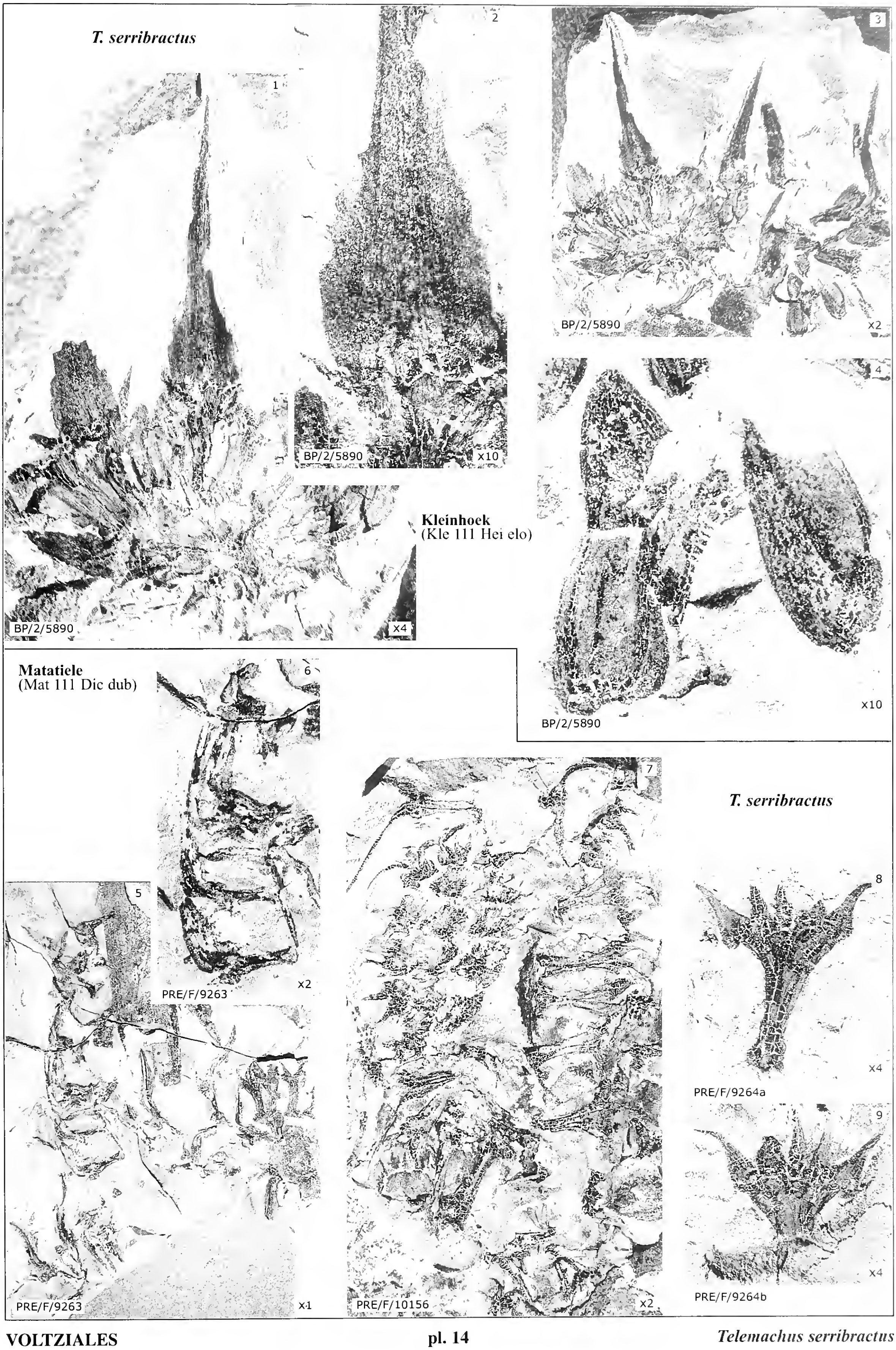


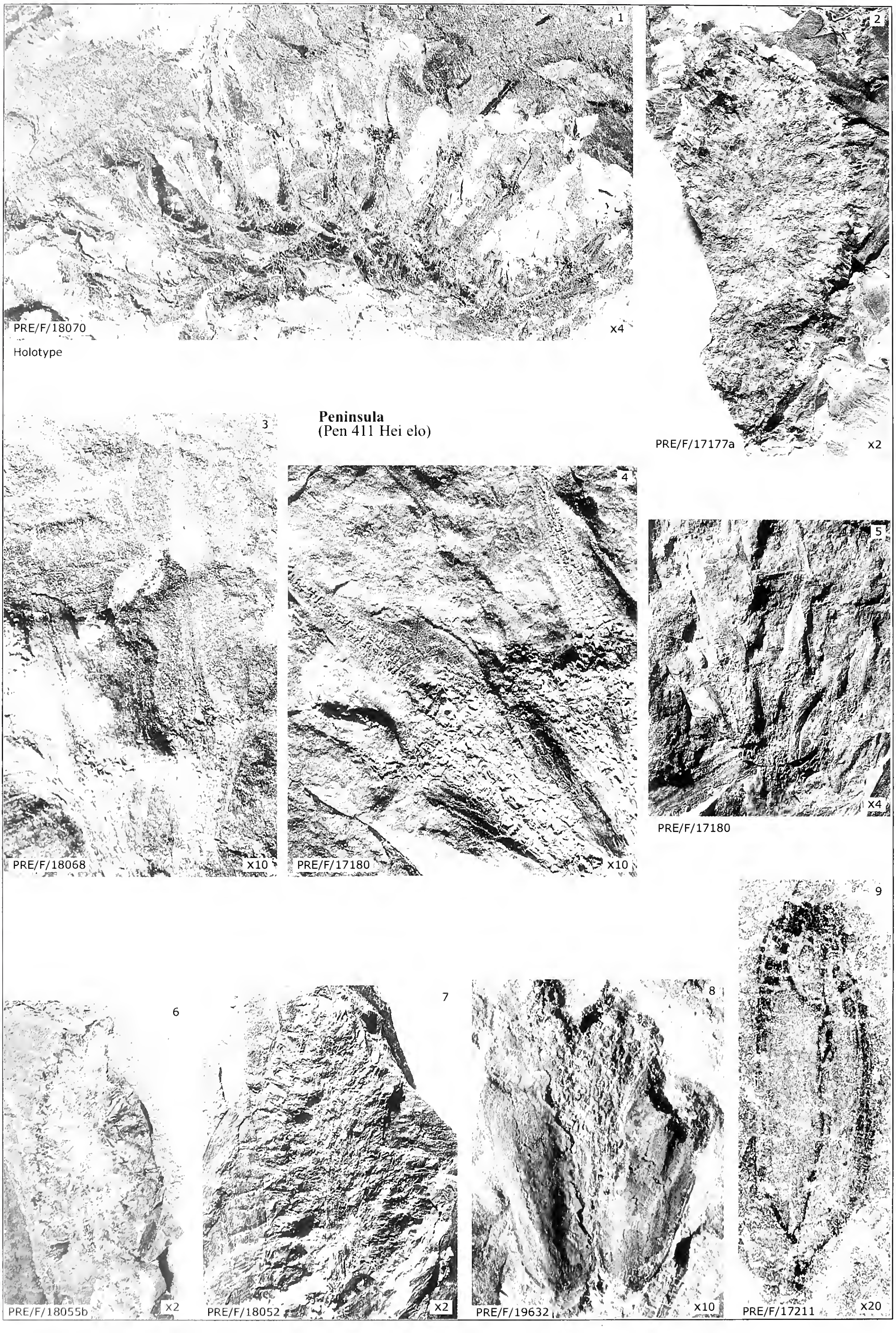
Telemachus elongatus **pl. 11** **VOLTZIALES**

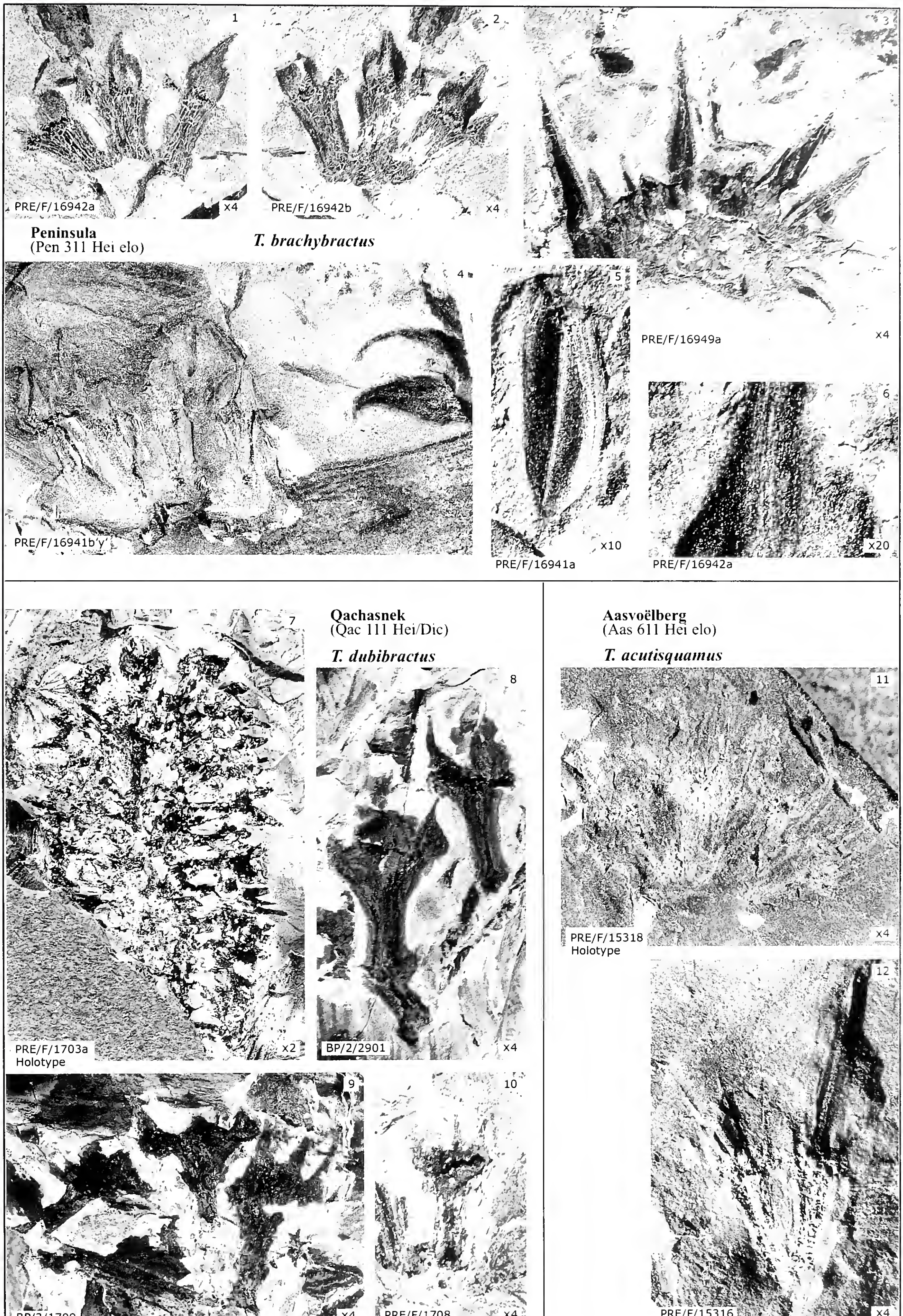

1
x1
PRE/F/20080a
Holotype
Kannaskop
(Kan 112 Hei elo)
2
PRE/F/20080b
x1
3
x2
PRE/F/20080a
4
x2
PRE/F/20082a
5
BP/2/3415
x4
T. grandis
Greenvale
(Gre 121 Hei elo)
T. elongatus
6
PRE/F/7750
x4
8
PRE/F/7738
x4
7
x2
PRE/F/7750
9
x2
PRE/F/7738
10
x2
PRE/F/19440
11
BP/2/4328
x4
Aasvoëlberg
(Aas 111 Hei elo)
T. elongatus
12
BP/2/4326
x2

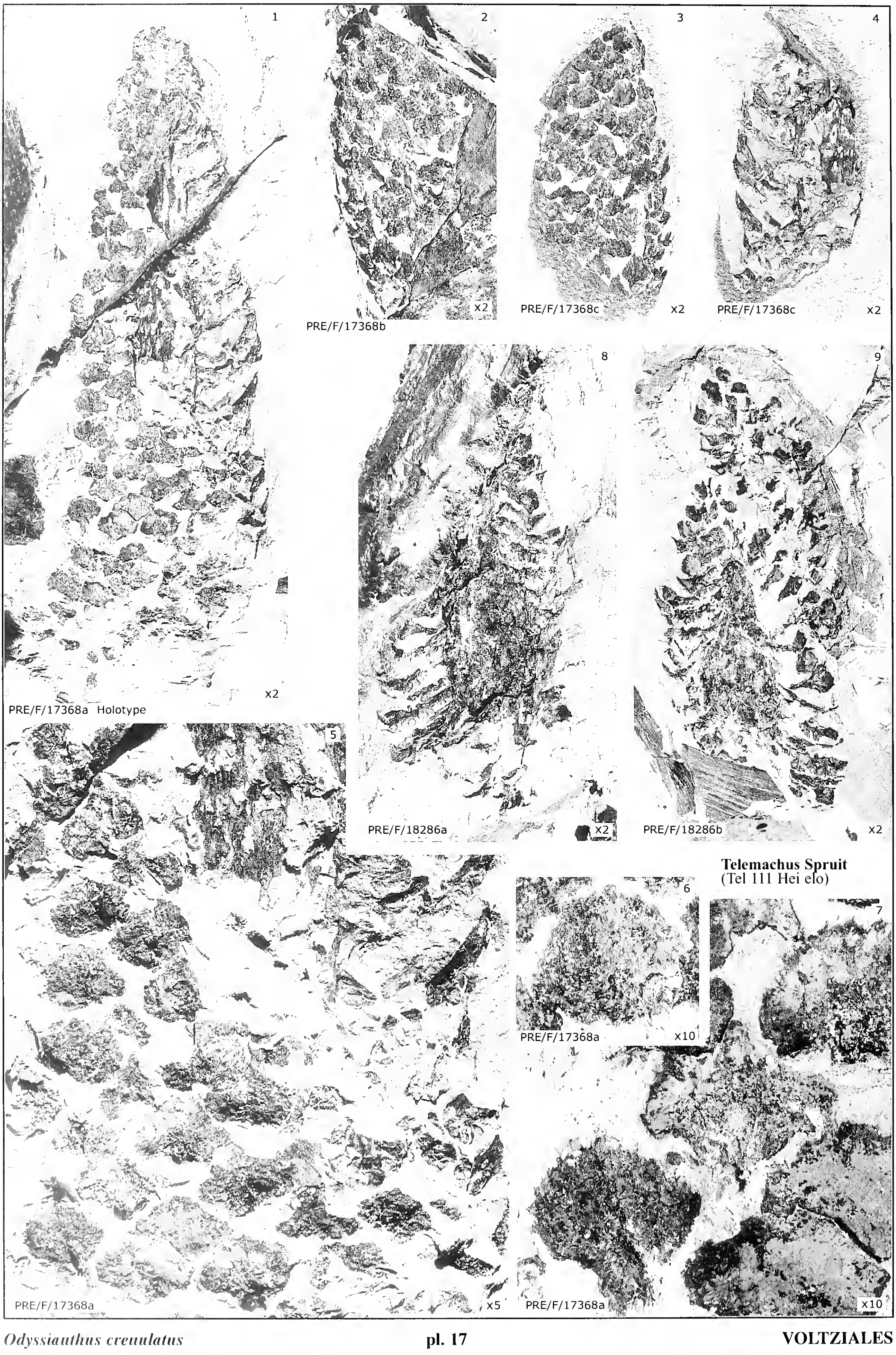


Telemachus serribractus **pl. 13** **VOLTZIALES**

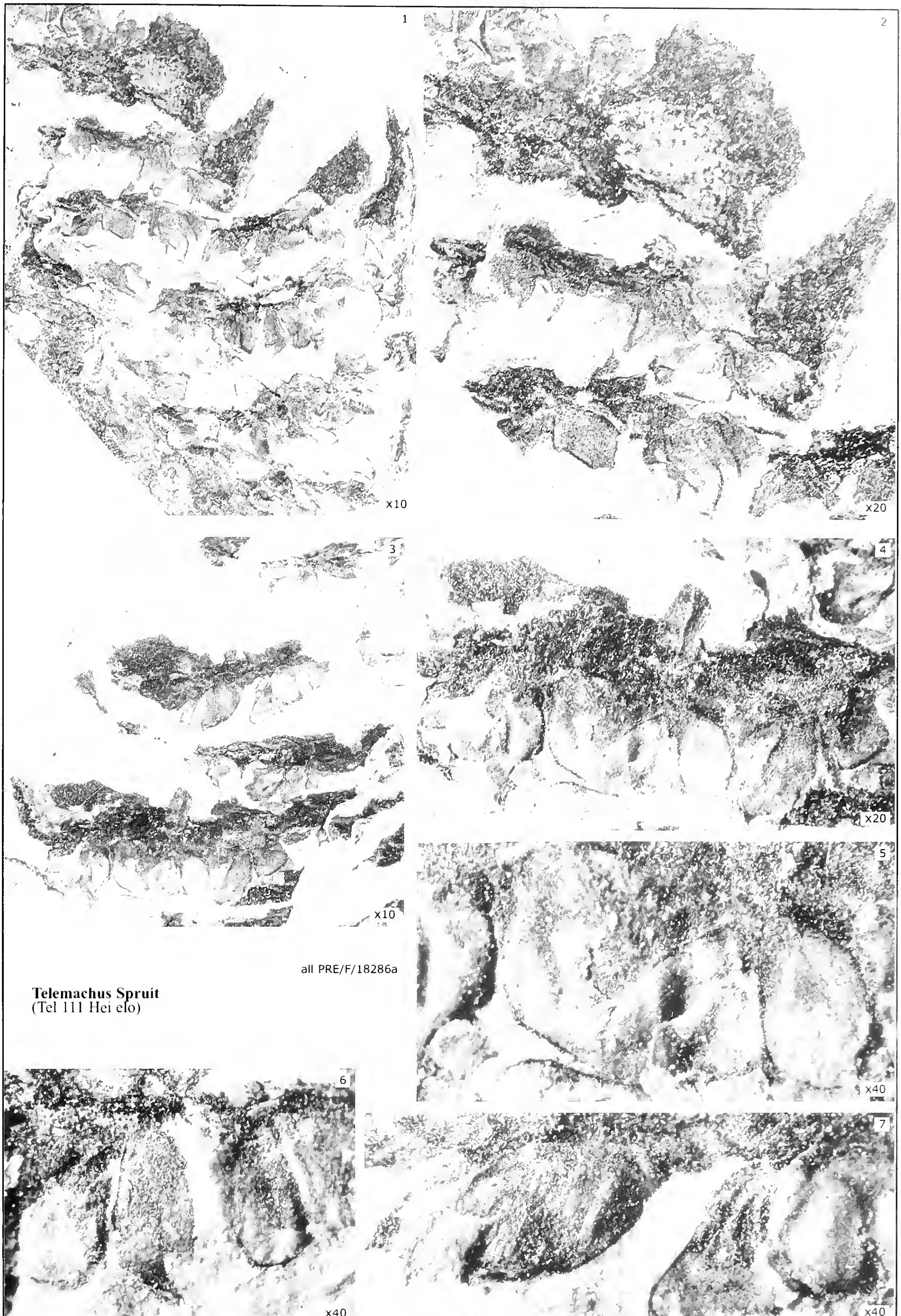

T. serribractus
1
BP/2/5890
x4
2
BP/2/5890
x10
3
BP/2/5890
x2
4
BP/2/5890
x10
Kleinhoek
(Kle 111 Hei elo)
Matatiele
(Mat 111 Dic dub)
5
PRE/F/9263
x1
6
PRE/F/9263
x2
7
PRE/F/10156
x2
T. serribractus
8
PRE/F/9264a
x4
9
PRE/F/9264b
x4


1
PRE/F/18070
x4
Holotype
2
PRE/F/17177a
x2
Peninsula
(Pen 411 Hei elo)
3
PRE/F/18068
x10
4
PRE/F/17180
x10
5
x4
PRE/F/17180
6
PRE/F/18055b
x2
7
PRE/F/18052
x2
8
PRE/F/19632
x10
9
PRE/F/17211
x20


1
PRE/F/16942a
x4
2
PRE/F/16942b
x4
3
PRE/F/16949a
x4
Peninsula
(Pen 311 Hei elo)
T. brachybractus
4
PRE/F/16941b'y'
5
x10
PRE/F/16941a
6
x20
PRE/F/16942a
7
PRE/F/1703a
Holotype
x2
Qachasnek
(Qac 111 Hei/Dic)
T. dubibractus
8
BP/2/2901
x4
9
BP/2/1709
x4
10
PRE/F/1708
x4
Aasvoëlberg
(Aas 611 Hei elo)
T. acutisquamus
11
PRE/F/15318
Holotype
x4
12
PRE/F/15316
x4



Odyssianthus crenulatus pl. 17 VOLTZIALES



all PRE/F/18286a

Telemachus Spruit
(Tel 111 Hei elo)

Clariphyllum J.M.And. & H.M.And., gen. nov.

Type species
Clariphyllum clarifolium J.M.And. & H.M.And. 1989, comb. nov.

Generic diagnosis
A voltzialean leaf of relatively small size, with *ca* 4 parallel veins, attached to shoots in a lax spiral arrangement without bracts.

Generic characters
Attachment: leaves in lax spiral, on long shoot, without bracts.
Leaf: individually dehisced, leaf small (75 x 3.5 mm), linear elliptic; tip rounded obtuse, base narrowly sessile; veins parallel, moderately spaced (10 per 10 mm), consistently at midlength, once forked near base, coalescing towards apex.
Cuticle: this vol., p. 101.

Eponymy
Clariphyllum: Clara's leaf, in honour of our eldest daughter who accompanied us on several collecting trips.

Global range: 1 sp., Gondwana, Tr. (CRN).
First & last: the single Molteno species described here.

Gondwana Triassic occurrence
Frequency (F): 3 degree squares (of the 84 across Gondwana).
Ubiquity (U): 1 continent (of 5 comprising Gondwana).
Diversity (D): 1 foliage species.
Abundance(A): <1% (the norm in Molteno TCs).
Longevity (L): 1 myrs (Carnian).
Colonisation success: FUDAL rating 3/1/1/–/1=6.
Minimum success (Grade 1): *Clariphyllum* was the 24th most prominent genus in the Gondwana Triassic; it was very low in frequency, ubiquity, diversity, abundance and longevity.
Endemism: the single species is endemic to the Molteno.

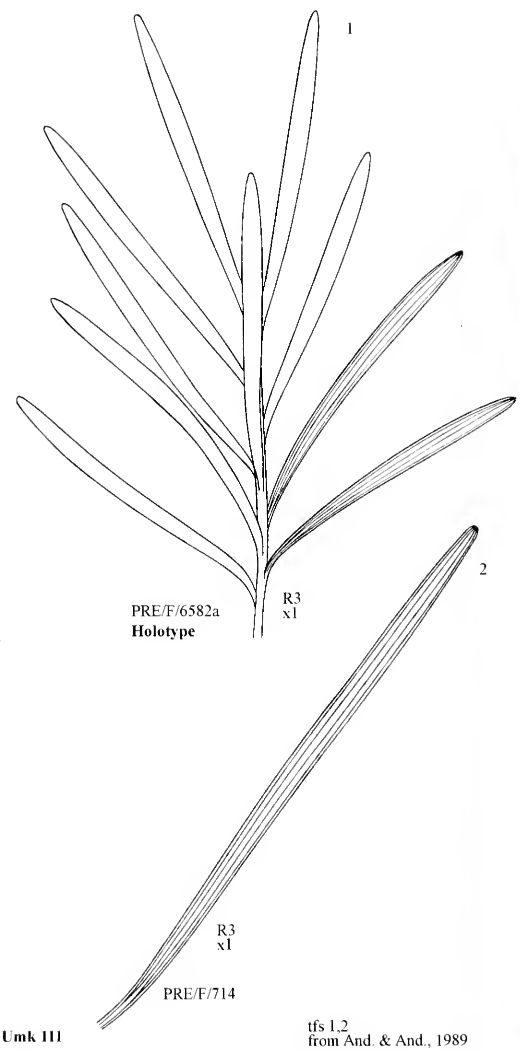
Molteno occurrence
Frequency (F): 3 TCs (of 100 sampled in Molteno).
Diversity (D): 1 species.
Abundance (A): 51 individuals total, rare to extremely rare.
Habit: probably a shrub.
Preferred habitat: *Dicroidium* riparian forest.

Affiliated organs
Female strobilus: unknown.
Male strobilus: unknown.

Classification & comparison
Intergeneric comparisons
Gondwana Triassic pinopsid genera—Clariphyllum was originally included by us in *Heidiphyllum* (And. & And. 1989), but considering the very different mode of attachment, the narrow leaflets and reduced number of veins, and the seemingly different cuticular preservation, this taxon is described here as a distinct genus. It is placed in the Voltziales on the general appearance of the individual leaves, but without any clue as to its affiliated female or male cones, or evidence of cuticular morphology, this cannot be verified.

Non-Gondwana genera—For discussion and comparison with *Tianshia patens* from the Middle Jurassic of China, see text for *Heidiphyllum* (p. 90).

C. clarifolium



Umk 111

tfs 1,2
from And. & And., 1989

Clariphyllum clarifolium J.M.And. & H.M.And. 1989, comb. nov.

Holotype
Specimen: PRE/F/6582 a,b; And. & And. [1989, pl. 264(10–12)].
Assemblage (TC): Umk 111 Dic 2spp; Umkomaas Valley.
Preservation: compression, a foliage shoot with *ca* 10 leaves, part and counterpart.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 20 indivs, And. & And. [1989, pl. 264(1–17)].

Sister palaeodemes—2 only.
Maz 211: 1 indiv.
Kap 111: 30 indivs.

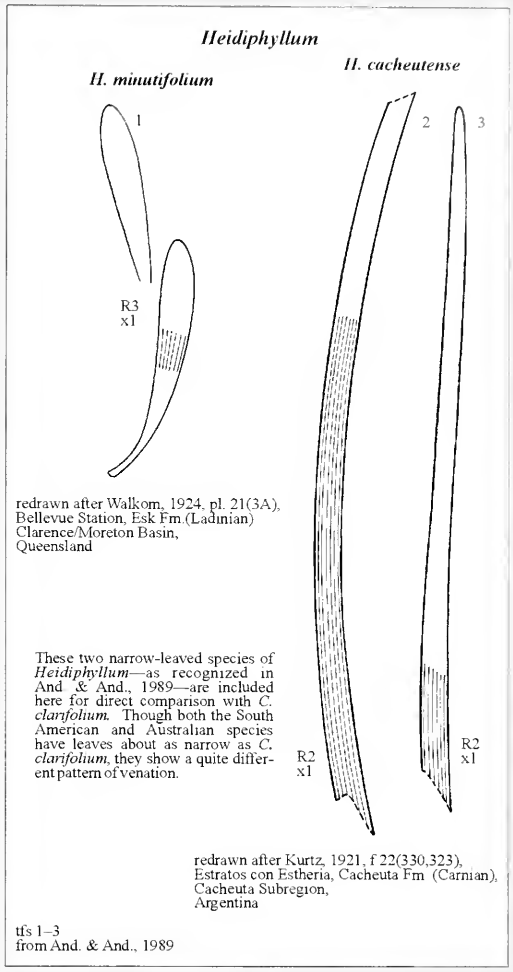
Specific diagnosis—as for genus.

Specific characters—as for genus.

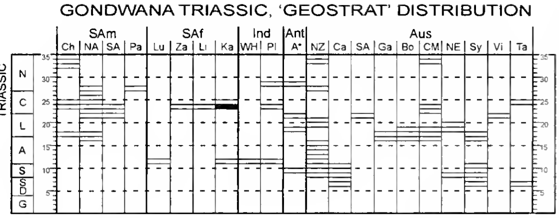
Eponymy
clariphyllum—for our daughter Clara who has accompanied us on several collecting trips.

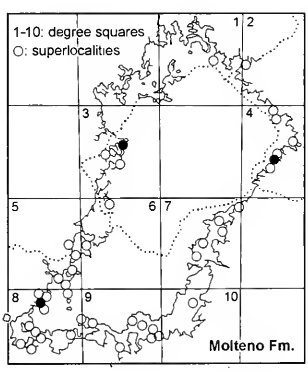
Comment & comparison
At Kap 111 and Maz 211 there have been found no attached leaves of this form and thus their generic identity needs future confirmation.

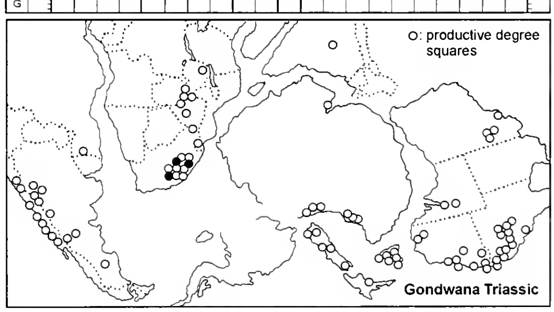
Cuticles
Potential sample: Lit 111, 20 indivs.
Macerated (this work): 9 indivs.
Preservation grade: Grade 1.
Diagnostic characters: none obtained.
Comment: —
Significance: of no value in classification and affiliation.



GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION







PINOPSIDA S.V.Meyen 1984
PINALES (Coniferales)
PODOCARPACEAE Endl. 1847

Rissikistrobus J.M.And. & H.M.And., gen. nov.

Type species
Rissikistrobus plenus J.M.And. & H.M.And., sp. nov.

Generic diagnosis
A pinalean female cone of linear shape with bract/scale complexes of 1–3 lobes bearing a pair of adaxial ovules on each lobe.

Generic characters
Attachment: terminal on leafy axis.
Strobilus: cone compact, linear (to *ca* 100 x 5 mm), megasporophylls spirally arranged, *ca* 6 units per gyre.
Megasporophyll: cone units consisting of ovuliferous bract/scale complexes; bracts leafy (to 5 mm), lanceolate, cuspidate, erect; scales, 1–3 lobed; ovules adaxial, paired, in concave surface of lobe.
Ovule: naked, (?)spathulate, 1.5 mm long.

Etymology
Rissikistrobus—after the affiliated foliage *Rissikia*.

Global range: 3 spp., Gondwana, Tr. (? – CRN).
First: *Rissikistrobus semireductus* (Retallack 1977); Cloughers Creek Fm. (UNEL 1564), Nymboida, Australia.
Last: the 3 Molteno species described here.

Gondwana Triassic occurrence
SAf—Karoo Basin, 8 TCs (*ca* 80 indivs).
Aus—Clarence Moreton Basin, 2 TCs (?indivs).

Although the affiliated foliage *Rissikia* occurs widespread in the Gondwana Triassic, *Rissikistrobus* (a single small fragment) has only been recorded from the Cloughers Creek Fm., Nymboida CM (Retallack *et al.* 1977) and according to K. Holmes (pers. comm.) also occurs in his collections from Basin Creek Fm., Nymboida CM Australia.

Molteno occurrence
Frequency (F): 7 TCs (of 100 sampled in the Molteno).
Diversity (D): 3 species.
Abundance (A): 85 individuals total, very rare to extremely rare.

Hla 212 Dic 3spp:	2 indivs in	11 man-hrs cleaving	(2 per 1 man-days)	very rare
Umk 111 Dic 2 spp:	45 " "	400 " "	(1 " 1 ")	"
Hla 213 Dic elo:	5 " "	60 " "	(1 " 1 ")	"
Kon 222 Dic edo:	2 " "	40 " "	(1 " 2 ")	"
Aas 411 Dic/Sph:	20 " "	512 " "	(1 " 2 ")	"
Kap 111 Dic/Ris:	3 " "	65 " "	(1 " 2 ")	"
Lit 111 Dic/Hei:	8 " "	550 " "	(1 " 6 ")	extr. rare

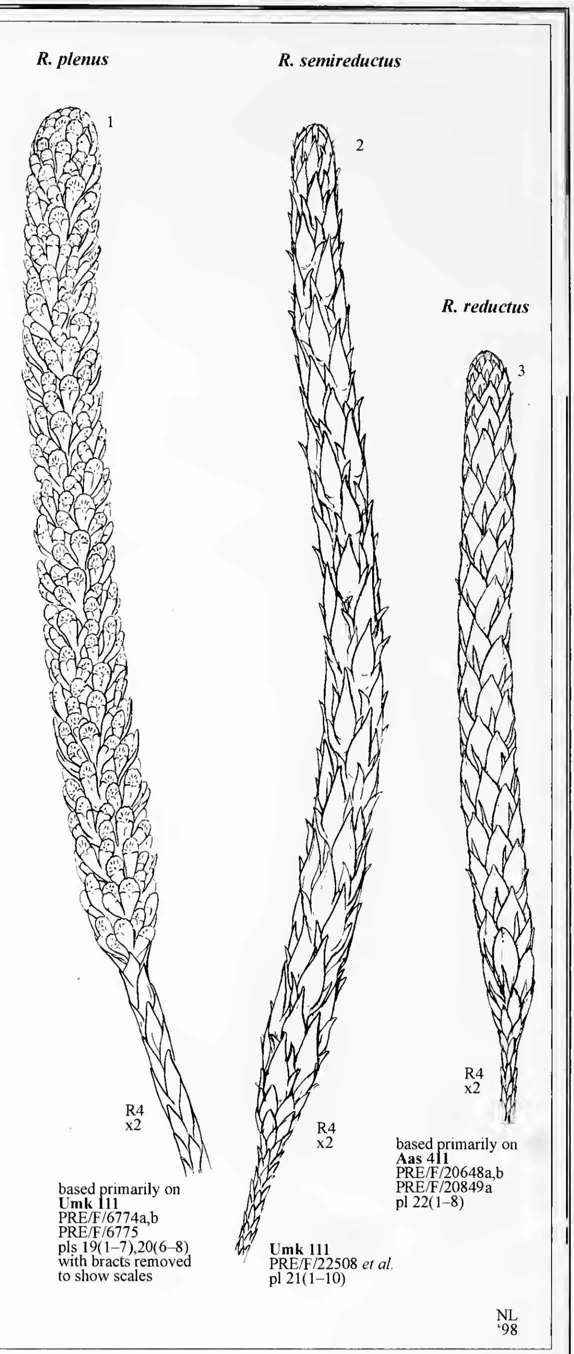
For details of the frequency and abundance of the three affiliated organs, *Rissikistrobus* (female), *Rissikianthus* (male) and *Rissikia* (female), through the Molteno, see Tab. 38 (p. 104); and for analysis of the mother plant's preferred habitat and of a typical TC (Pen 321 Dic/Ris) in which it occurs as a co-dominant, see And. & And. (in prep.).

Affiliated organs
Female: *Rissikistrobus*—Grade 4 (Cut. cor., Mut. occ.).
Foliage: *Rissikia*—Grade 4 (Cut. cor., Mut. occ.).

The affiliation of fruit (male and female) and foliage, based on the distribution data tabulated for the Molteno (Tab. 38, p. 104), is virtually certain. Townrow (1967) established to his satisfaction that the cuticle of the three organs corresponded. We have not attempted to verify his results based on specimens from our collection (see further on pp. 104, 105).

Classification & comparison
Suprageneric classification (Podocarpaceae/Pinales)

It might be expected that within the initial Triassic radiation of the Pinales (pp. 56, 57), during which six of the eight extant families are generally accepted to have emerged, there would be encountered many archaic and transitional features within the evolving lineages. This seems to be well exemplified, for instance, in the *Rissikistrobus/Rissikia* plant, where characters of the sister families Pinaceae and Podocarpaceae are both in evidence. Considerable published debate (p. 105) has been devoted to which of the two families is represented by this widespread Gondwana Triassic genus (see map for *Rissikia*, p. 113). The debate is not settled and we have wavered this way and that, settling, for now, with no great conviction on the Podocarpaceae.



Reconstructions

For each of the three species, *R. plenus*, *R. semireductus* and *R. reductus*, an R4 grade reconstruction has been made and each is based on one or two particular specimens along with the rest of the reference palaeodeme for the taxon.

The precise nature of the scale/bract complexes in the three recognised species of *Rissikistrobus* has not been unambiguously established—as is demonstrated in the degree to which we differ from the morphological interpretations of Townrow (1967) outlined on p. 105. Our various reconstructions of both the megasporophylls and the full cones should be accepted in this light. No doubt more cuticular studies of the reasonably numerous Umkomaas (Umk 111) and Little Switzerland (Lit 111) specimens together with sectioning of the casts/moulds of the Aasvoëlberg (Aas 411) specimens, should go a long way towards clarifying the structure.

Molteno occurrence (elaborated)

Mother plant (Rissikistrobus/Rissikia/Rissikianthus)

The habit and preferred habitat of the mother plant of *Rissikia media*, by far the more frequent and abundant of the two Molteno foliage species, is analysed in some detail in a sequel to this work (And. & And., in prep.). It is visualised as being a substantial, scattered tree in *Dicroidium* riparian forest or *Dicroidium* open woodland, occasionally forming monodominant wetland stands.

Foliage (Rissikia)

Rissikia occurs in 21 of the 100 Molteno TCs and in all but one instance in assemblages dominated by *Dicroidium*—in riparian forest and open woodland. Generally the genus is rare (<1%), but in five TCs it does become fairly common (1–5%) and in two TCs it is a co-dominant (30–40%). In the latter two instances, *Rissikia* is seen as forming a distinct vegetation type—akin to the swamp cyprus—within the open woodland.

Female cone (Rissikistrobus)

The female cone (*Rissikistrobus*) occurs in eight TCs, twice as often as the male. It clearly appears more often in the riparian forest TCs than elsewhere. Even where the male and female occur in the same assemblage, their abundance tends to be very unbalanced, either the one way or the other.

Male cone (Rissikianthus)

The male cone (*Rissikianthus*) occurs in only five TCs: essentially once in each vegetation type—and in each case where the foliage is most common for that habitat. The conclusion drawn from this is that the male occurs only autochthonously or very nearly so. Interestingly, in the two instances (Kap 111 & Pen 321) where the foliage is particularly abundant, the male is clearly more common than the female.

Gondwana Triassic occurrence (elaborated)

Whole-plant genus (Rissikistrobus/Rissikia/Rissikianthus)

The whole-plant genus is well established on the basis of the secure affiliation (Grade 4) of all three organs—foliage, female cone and male cone. While the 'genus', through its foliage, is known to have occurred widespread across Gondwana, the reproductive organs remain virtually unknown beyond the Molteno.

Foliage genus (Rissikia, pp. 112, 113)

Rissikia has been established in this volume (Tab. 20, p. 27) as the 11th most prominent of the 27 Molteno gymnospermous foliage genera in the Gondwana Triassic. With a FUDAL rating (colonisation success) of 39, it occurred ubiquitously across Gondwana during the upper half of the Triassic, being recorded from no less than 11 degree squares outside 'Africa'. Its abundance is not recorded in the literature, but it probably occurred only as an occasional element in most TCs (1–2%) as in the Molteno; and it reflected little diversity (two species).

Ovulate-cone genus (Rissikistrobus)

In marked contrast to the foliage, *Rissikistrobus* has been recorded, aside from Africa, only in eastern Australia: one published and one unpublished record from the Nymboida Coal Measures (Retallack *et al.* 1977; Holmes, pers. comm.).

Pollen-cone genus (Rissikianthus, pp. 108, 109)

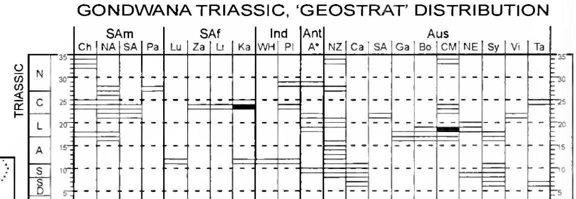
As for the other four pinopsid male-cone genera recorded in the Molteno, *Rissikianthus* remains unknown elsewhere in Gondwana.

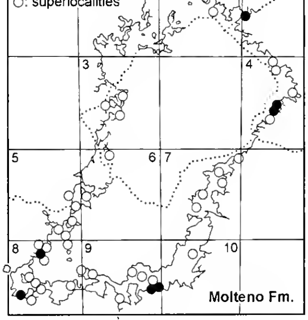
Tab. 37.

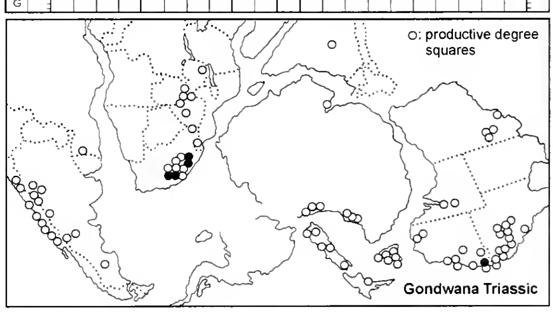
RISSIKISTROBUS HYPODIGM, Gondwana Triassic occurrence

AUTHOR		SUBREGION		FORMATION		LOCALITY	NAME	Indivs	ILLUSTRATION	Species: Molteno: *R. plenus*	*R. semireductus*	*R. reductus*	*R. spp. indet*	Intact-ness: Intact strobili	Fragmentary "	Isolated megasp.
SOUTH AFRICA																
1967	Townrow	Underberg	KA9	24	Molteno	Umkomaas	*Rissikia media*	2	pl 1(A,B), tf 8(C-J)	-	2	-	-	2	-	-
"	"	"	"	"	"	"	" *apiculata*	1	pl 1(C,D), tf 8(D)	-	-	1	-	1	-	-
1978-1999 Anderson & Anderson Molteno literature not included in this table																
AUSTRALIA																
1977	Retal. *et al.*	Nymboida	CM7	19	Cloughers Cr.	UNEL 1564 (Kang.Cr.)	*Rissikia media*	1	f I1(A)	-	-	-	1	-	1	-

GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION







assemblages (taphocoenosis)	*Rissikia*	♀ *Rissikistrobus*	*R. plenus*	*R. semireductus*	*R. reductus*	Incertae	♀ seeds (in-situ)	♂ *Rissikianthus*	*R. concavus*	*R. linearis*	*R. townrowii*	*R. convectus*	Incertae	♂ microsporangia (in-situ) *
Boe 112 Dic cor	12	-	-	-	-	-	-	1	-	-	-	-	1	1
Tin 121 Sph 2spp	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Kon 223 Dic odo	4	-	-	-	-	-	-	-	-	-	-	-	-	-
" 222 " "	9	2	-	-	-	2	-	-	-	-	-	-	-	-
" 111 " "	**2**	-	-	-	-	-	-	-	-	-	-	-	-	-
Pen 321 Dic/Ris	**35**	-	-	-	-	-	-	30	30	-	-	-	-	7
" 211 Dic/Equ	1	-	-	-	-	-	-	-	-	-	-	-	-	-
" 221 Dic/Equ	2	-	-	-	-	-	-	-	-	-	-	-	-	-
" 421 Dic odo	5	-	-	-	-	-	-	-	-	-	-	-	-	-
Kle 111 Hei/Dic	3	-	-	-	-	-	-	-	-	-	-	-	-	-
Kap 111 Dic/Ris	**38**	3	-	-	-	3	-	25	-	-	-	25	-	5
Nuw 111 Dic zub	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Hla 211 Dic 3spp	**1**	-	-	-	-	-	-	-	-	-	-	-	-	-
" 212 Dic 3spp	**1**	2	-	2	-	-	-	-	-	-	-	-	-	-
" 213 Dic elo	**2**	5	3	2	-	-	2	-	-	-	-	-	-	-
Umk 111 Dic 2spp	**5**	45	4	41	-	-	4	8	-	-	8	-	-	2
Mng 111 Dic 2spp	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Lit 111 Dic/Hei	40	8	-	-	-	8	-	-	-	-	-	-	-	-
Aas 311 Hei elo	1	-	-	-	-	-	-	-	-	-	-	-	-	-
" 411 Dic/Sph	25	20	-	-	20	-	-	15	-	15	-	-	-	5
Bam 111 Dic dub	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Total TCs	21	7	2	3	1	3	2	5	1	1	1	1	1	5
Total indivs	%	85	7	45	20	13	6	79	30	15	8	25	1	20

* microsporangia clearly evident

Tab. 38. *Rissikistrobus/Rissikia*, Molteno occurrence

Evidence for affiliation of organs

Short of organic attachment, the affiliation of foliage (*Rissikia*), seed cone (*Rissikistrobus*) and pollen cone (*Rissikianthus*) is as securely established as can be expected.

Mutual occurrence

Rissikia, a relatively frequent component of the Molteno flora, occurs in 21 TCs (Tab. 38). *Rissikistrobus* occurs in seven TCs, invariably in co-occurrence with *Rissikia*, while *Rissikianthus* occurs in five TCs, also invariably together with the foliage, though in only three of these, along with the ovulate cone. Overall, in the context of fossil floras, this amounts to particularly strong evidence for three-way affiliation.

Retallack *et al.* (1977) records *Rissikia* leaves from eastern Australia and a female cone from the same locality (Tab. 37). This is here regarded as *Rissikistrobus* sp. indet. and provides further evidence of mutual occurrence.

Cuticular correspondence

In support of the evidence based on co-occurrence, the strong similarity between the cuticles of the foliage and the reproductive organs *Rissikistrobus* and *Rissikianthus* (see sketches opposite and on p. 112) provides convincing proof of affiliation.

Nomenclature (as relates to affiliation)

Holotype: Townrow (1967) originally described the female cone together with the male counterpart and foliage as *Rissikia media*. We have retained his name for the leaves and introduce new names here for the female and male cones. Townrow never nominated a holotype but did suggest that Burnera Waterfall (i.e. Umk 111) be considered the *locus typicus*.

Intactness & preservation of cones (Molteno)

In situ *seeds*

The seeds of *Rissikstrobus*, unlike those of *Telemachus*, are nowhere satisfactorily preserved in the Molteno collection. In only four cones from Umk 111 and two from Hla 213 are the very small, featureless, spathulate seeds/ovules seen *in situ*. In the remainder of the 86 available cones, the seeds have either not developed to maturity or have been dispersed, or the material is insufficiently preserved.

Dispersed seeds

The *Rissikistrobus* seed is very much the same size and shape as the microsporangium of *Stachyopitys* sp. A. Only under the microscope, considering the fingerprint ornamentation of the latter and the featurelessness of the former, are they distinguishable. We have not scanned slabs from the *Rissikia*-yielding TCs microscopically to establish the extent of occurrence of dispersed *Rissikistrobus* seeds.

Cuticles

Potential sample: Umk 111, 45 indivs.
Macerated (this work): nil.
Preservation grade: Grade 4–5.
Diagnostic characters: see Townrow (1967); this vol., p. 105.
Comment: as for *Rissikianthus* (p. 109).
Significance: as for *Rissikianthus* (p. 109).

Adaptive radiation (Molteno diversity)

Identifying species within the genus is difficult and the conclusions reached here need to be verified by cuticular studies. Only two reasonably comprehensive and well-preserved palaeodemes (Umk 111 & Aas 411) are at hand. Though the affiliated foliage, *Rissikia*, from the two TCs appears very alike, suggesting the presence of a single species, the female cones are significantly different.

As in *Telemachus*, it is in the scale/bract complexes that the differences between the species appear. A reduction series seems to be revealed in the cones from Umk 111 and Aas 411—from scales with three deeply divided equal-sized lobes through forms with strongly reduced lateral lobes, to those at Aas 411 (clearly) and at Umk 111 (less clearly) where only the central lobe occurs. Three species are provisionally recognised. It is not impossible that the Umkomaas (Umk 111) species are, in fact, members of a morphological or ontogenetic series.

The three Molteno species are based on the following TCs/reference palaeodemes.

R. plenus—Umk 111 Dic 2spp (Umkomaas Valley), 4 indivs
Dicroidium riparian forest (mature); Cycle 2b (Indwe Member)
R. semireductus—Umk 111 Dic 2spp (Umkomaas Valley), 41 indivs
Dicroidium riparian forest (mature); Cycle 2b (Indwe Member)
R. reductus—Aas 411 Dic/Sph (Aasvoëlberg), 20 indivs
Sphenobaiera closed woodland; Cycle 1 (Bamboesberg Member)

Townrow (1967) on *Rissikistrobus/Rissikia* classification

Affinity with the Podocarpaceae

After an exhaustive comparative study between *Rissikia* (with its cone affiliates) and the extant coniferalean families, Townrow (1967) concluded that this Triassic genus could be referred, at least 'for the present', to the Podocarpaceae, and that 'the only family that otherwise enters the picture is the Pinaceae'. He added that 'even though this does involve a slight widening of the limits of the family.........confusion is unlikely, for the modification needed is small. The alternative would be a new family, and there seems no object in this.' There follows, in briefest outline, Townrow's more obvious morphological considerations supporting his conclusion.

Female cone—a) The spike-like cone of '*Rissikia*' is seen in the podocarps *Dacrydium franklinii*, *Podocarpus spicatus* and *P. andinus*, but in no other extant conifer family; b) the 3-partite scale of '*Rissikia*' is faintly reflected in the reduced, 3-pointed scales of the podocarps *D. franklinii*, *Michrocachrys* and *Saxegothea*; c) in *Podocarpus spicatus* and *P. andinus*, a double vascular trace—as 'possibly' occur in each scale lobe of '*Rissikia*'—proceeds 'past the chalaza into the further part of the epimatium'.

Male cone—a) The two pollen sacs (per scale) and disaccate pollen of '*Rissikia*' are found with regularity in the Podocarpaceae and Pinaceae only; b) 'the corpus and saccus shape and ornamentation seem .... to come close to *Dacrydium*'. ('Striae are not known in any living conifer.')

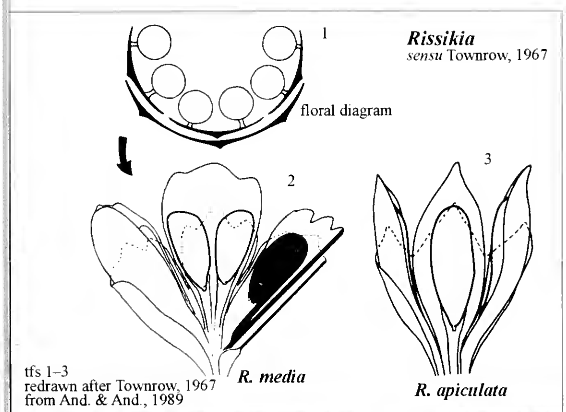
Foliage—a) Long and short shoots, as occur in '*Rissikia*', are found in only a few living conifers falling in three families—*Metasequoia* and *Taxodium distinctum* (in the Taxodiaceae), *Larix* and *Cetrus* (in the *Pinaceae*), and *Acmopyle*, some *Podocarpus* species and perhaps *Polypodiopsis* (in the Podocarpaceae); b) the bilateral leaves characteristic of *Rissikia* 'are found today only in the Podocarpaceae'; c) 'the very thin leaves with four stomatal zones each only one stoma wide can be seen in young *Dacrydium novoguineense*', while 'the stomatal details of *Rissikia*' recall the podocarps *Saxegothea* and *Microstrobos* 'especially' (though comparison with *Metasequoia* in the Taxodiaceae is also possible).

Townrow (1967) reconstructions of Rissikistrobus

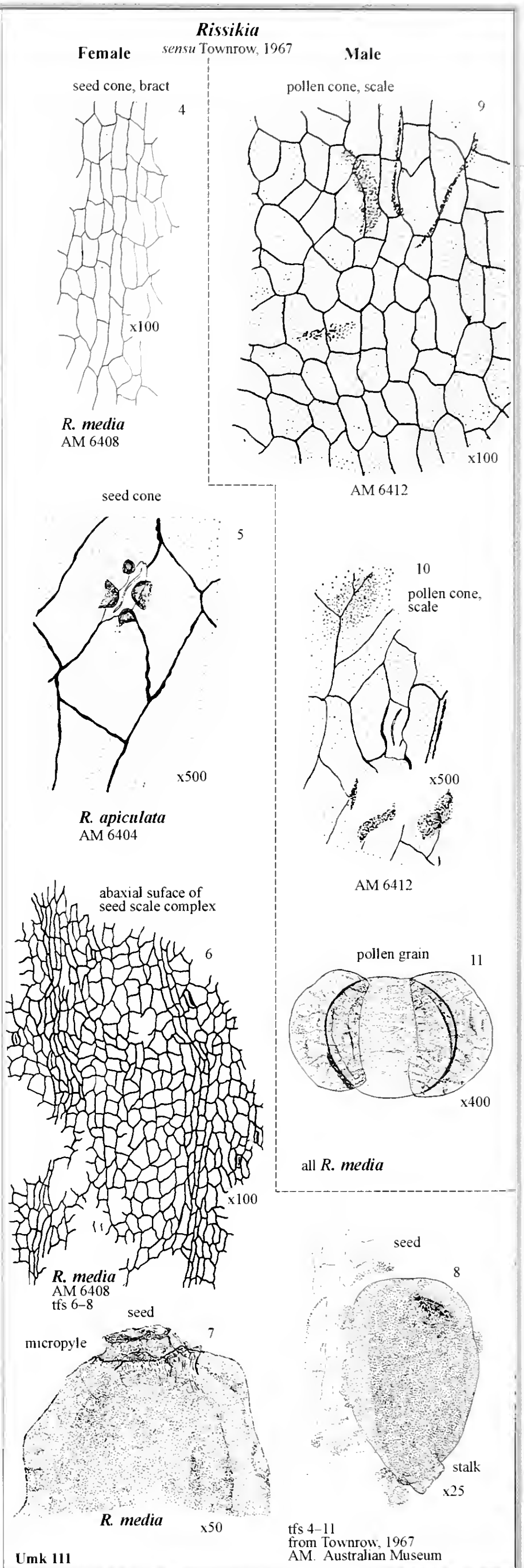
On the basis of his detailed morphological study of six compression specimens from Umk 111 (collected by himself and now housed in the Australian Museum, Sydney), Townrow (1967) concluded that the female cone *Rissikistrobus* was best included in the extant family Podocarpaceae. If correct, *Rissikistrobus* and its affiliates would constitute the first appearance of the family (Cleal 1993; and see pp. 57).

This work of Townrow has been cited frequently since by authors writing on the fossil conifers (e.g. Miller 1977; Taylor *et al.* 1987; Stewart & Rothwell 1993; Taylor & Taylor 1993) with varying degrees of agreement concerning the podocarpaceous affinities of the material. Miller (1977), for instance, concluded that *Rissikia* 'would probably have been classified in the Voltziales had it not been for the podocarpaceous foliage and the ease with which we can envision the possible evolution of the known Jurassic forms of the Podocarpaceae from this genus'.

We follow Townrow's interpretations with uncertainty. For instance, *Compsostrobus* from the Late Triassic Pekin Fm. of North Carolina, U.S.A., which Taylor *et al.* (1987) place, with reservations, in the Pinaceae has features reminiscent of *Rissikistrobus*.



tfs 1–3
redrawn after Townrow, 1967
from And. & And., 1989



tfs 4–11
from Townrow, 1967
AM. Australian Museum

Rissikistrobus plenus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/6774a,b; tf. 1a,b, adjacent, pl. 19(1–7).
Assemblage (TC): Umk 111 Dic 2spp; Umkomaas Valley.
Preservation: incomplete cone (proximal end missing), part and counterpart, longitudinal outer view showing many scales with *in situ* ovules; compression in thinly laminated, carbonaceous (good cuticle) moderately baked, dark grey shale with good cleavage.

Reference palaeodeme
Assemblage: as for holotype.
Specimens: 4 indivs (4 intact cones).

Sister palaeodemes—1 only.
Hla 213 Dic elo: 3 intact cones.

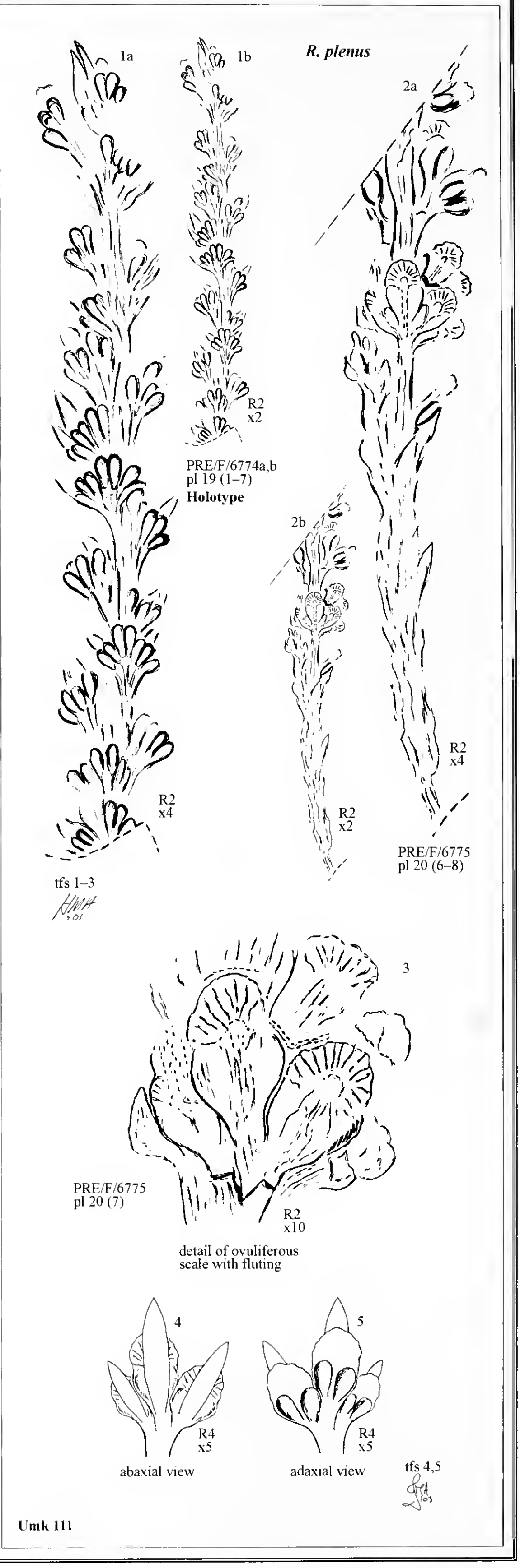
Specific diagnosis
A *Rissikistrobus* species with an ovuliferous scale consisting of 3 nearly similar-sized lobes.

Specific characters
Strobilus: long (to *ca* 80 mm).
Megasporophyll: bracts distinctly longer than scales; scales 3-lobed, with outer lobes slightly reduced.
Ovule: tear-shaped (*ca* 1 x 0.5 mm).

Etymology
plenus (Lat.)—full, complete, with reference to the lobed scales.

Comment & comparison
The bract/scale complex in this species is particularly difficult to interpret. The R4 reconstructions (tfs 4, 5, adjacent) are based on the two most explicit specimens of the reference palaeodeme. Each shows different features. In the holotype, PRE/F/6774a,b (tf. 1a,b, adjacent), the three ovule pairs are seen clearly preserved in several places, as are the lanceolate bracts. In PRE/F/6775 [tf. 2a,b, adjacent; pl. 20(6–8)], the distinctively fluted, semicircular, distal halves of the three scale lobes are seen fortuitously preserved in only one area (a further specimen, PRE/F/6759b, pl. 20(3–5), shows the feature less clearly.) Apparently in the fully mature specimens, or in fossilisation, the distal lamina of the scale detaches leaving the three pairs of ovules—still attached to the spreading stalk—exposed.

It is possible that the two Umkomaas (Umk 111) species, *R. plenus* and *R. semireductus*, represent parts of a morphological continuum or ontogenetic series and should be combined as one taxon. There does exist a very wide morphological range of *Rissikia* foliage (And. & And. 1989, pls 265–271) at both Umk 111 and Hla 213 (also including both *Rissikistrobus* species) which may support the two-species option preferred here. Also, the recognition of a third species, *R. reductus*, characterised by the lone central lobe, does suggest the likelihood of a morphologically intermediate species.



Rissikistrobus semireductus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/22508; pl. 21(1–5).
Assemblage (TC): Umk 111 Dic 2spp; Umkomaas Valley.
Preservation: incomplete cone, without counterpart, longitudinal outer view showing several scales and a few *in situ* ovules; compression in thinly laminated, carbonaceous (good cuticle) moderately baked, dark grey shale with good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 41 indivs (4 intact cones, 37 partial cones).

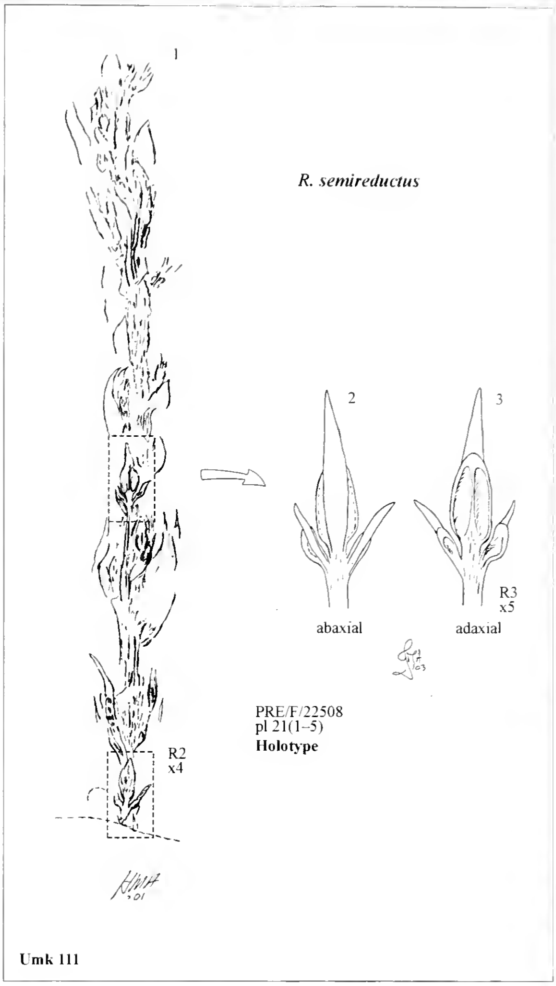
Sister palaeodemes—2 only.
Hla 212 (1 intact & 1 partial cone).
Hla 213 (2 intact cones).

Specific diagnosis
A *Rissikistrobus* species with an ovuliferous scale consisting of a large central lobe and two very reduced lateral lobes.

Specific characters
Strobilus: long (to *ca* 85 mm).
Megasporophyll: bracts distinctly larger than scales; scales 3-lobed, with outer lobes strongly reduced.
Ovules: linear-elliptical (*ca* 2 x 0.5 mm).

Etymology
semireductus (Lat.)—with reference to the semireduced lateral lobes.

Comments & comparison
The structure of the *R. semireductus* bract/scale complex in external and lateral view is most clearly visible in the holotype. The two best preserved units, as indicated in tf. 1 adjacent, are reconstructed (R3) at higher magnification (tfs 2, 3) in abaxial and adaxial view. The additional 40 cones and cone fragments included in this species do not add a great deal and some may well belong to *R. plenus*.



Rissikistrobus reductus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/20648a,b; pl. 22(3–7).
Assemblage (TC): Aas 411 Dic/Sph; Aasvoëlberg.
Preservation: fairly complete cone (proximal end missing), part and counterpart, longitudinal outer view and part section showing many scales and a few *in situ* ovules; 3D mould and cast, imperfectly preserved; impression in thinly laminated, strongly baked, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 20 indivs (2 complete & 18 partial cones).

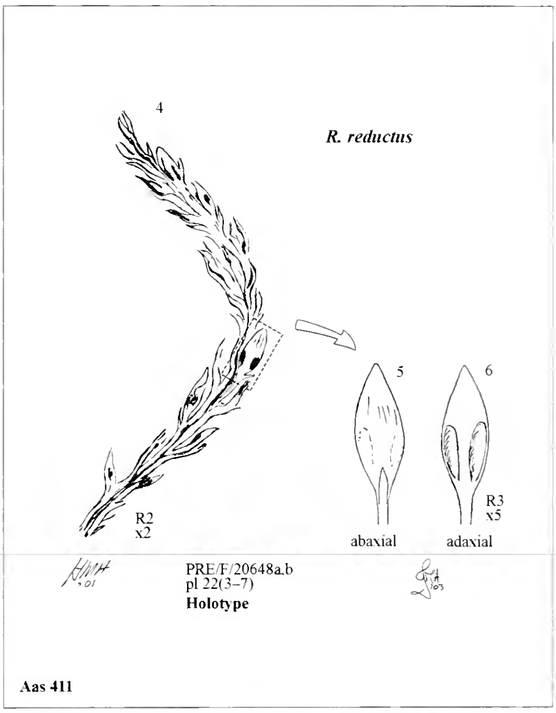
Sister palaeodemes—nil.

Specific diagnosis
A *Rissikistrobus* species with an ovuliferous scale consisting of a single lobe.

Specific characters
Strobilus: relatively short (to *ca* 60 mm).
Megasporophyll: bracts reduced, far shorter than scales; scales unlobed [(?)outer lobes lost].
Ovule: linear-elliptical (*ca* 0.8 x 0.35 mm).

Etymology
reductus (Lat.)—with reference to the completely reduced lateral lobes.

Comments & comparison
The type locality, Aas 411, has yielded a good palaeodeme of *Rissikistrobus* cones that are quite distinct from the Umk 111 specimens. We are obviously dealing with a separate species, though this is not evident in the affiliated *Rissikia* foliage.



Rissikianthus J.M.And. & H.M.And., sp. nov.

Type species
Rissikianthus townrowii J.M.And. & H.M.And., sp. nov.

Generic diagnosis
A pinalean male cone of small size (*ca* 10–18 mm long) with microsporophylls bearing a pair of horizontally aligned abaxial microsporangia.

Generic characters
Strobilus: a compact cone, lanceolate to elliptical, of small size (10–18 mm long); axis relatively gracile, strongly flexed towards base, with short to long foliated free end; microsporophylls helically attached, in 7–10 gyres of *ca* 6–12 units (at midlength).

Microsporophyll: a simple scale, proportionately intermediate in length, more or less straight, at 90° from axis; distal lamina woody, variously triangular, entire, with strong heel; stalk broadly tapering proximally, winged and keeled; microsporangia abaxial, two in number, extending horizontally from heel of distal lamina, sessile.

Microsporangium: rotund (*ca* 2 x 1 mm), shallowly longitudinally bilobed.

Pollen: striate disaccate.

Etymology
Rissikianthus—emphasising affiliation with the foliage *Rissikia*.

Global range: 4 spp., Gondwana, Tr. (CRN).
First & last: the 4 Molteno species described here.

Gondwana Triassic occurrence
SAf—Karoo Basin, 5 TCs (79 indivs).

Molteno occurrence
Frequency (F): 5 TCs (of 100 sampled in the Molteno).
Diversity (D): 4 species.
Abundance (A): 79 indivs total, rare to extremely rare.

Pen 321 Dic/Ris:	30 indivs in	35 man-hrs cleaving	(10 per 1 man-day)	rare
Kap 111 Dic/Ris:	25 " "	65 " "	(3 " 1 ")	very rare
Boe 112 Dic cor:	1 " "	6 " "	(1 " 1 ")	"
Aas 411 Dic/Sph:	15 " "	512 " "	(1 " 3 ")	"
Umk 111 Dic 2spp:	8 " "	400 " "	(1 " 5 ")	extr. rare

While the three genera of Molteno voltzialean male cones are all extremely rare, those of *Rissikianthus* are markedly more frequent and common.

Affiliated organs
Female strobilus: *Rissikistrobus*—Grade 4 (Kin. reinf., Mut. occ.).
Foliage: *Rissikia*—Grade 4 (Kin. reinf., Mut. occ.).

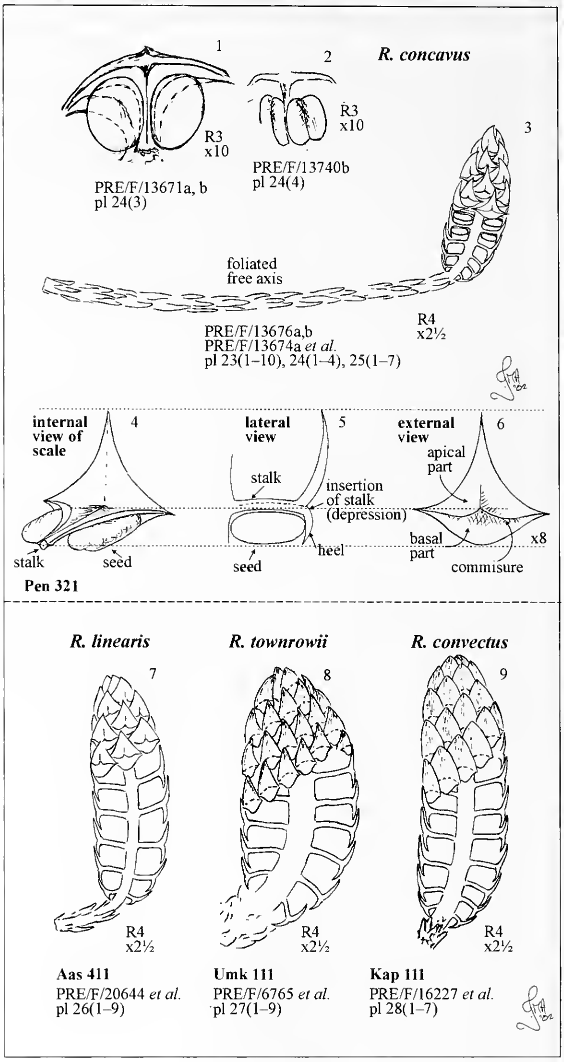
Though nowhere known in organic connection, the affiliation of *Rissikistrobus, Rissikianthus* and *Rissikia* is considered virtually certain (see further on pp. 104, 105).

Classification & comparison
Suprageneric classification (Podocarpaceae/Pinales)

Townrow (1967) records that cones with two pollen sacs and disaccate pollen as in *Rissikianthus* (his *Rissikia)* are found with regularity only in the Podocarpaceae and Pinaceae. With regard to the pollen, he records that 'the corpus and saccus shape and ornamentation seem .... to come close to *Dacrydium*.' He states further that striae, which characterise the *Rissikianthus* pollen 'are not known in any living conifer.' Townrow concludes, along with evidence from the female cone and the foliage, that the *Rissikia/Rissikistrobus/Rissikianthus* plant represents the earliest known member of the Podocarpaceae (see fuller discussion on p. 105).

Intergeneric comparison (Molteno genera)

Five pinopsid (coniferopsid) male cone genera have been recognised here in the Molteno: *Fredianthus*, *Lutanthus* and *Odyssianthus* included in the Voltziales; *Rissikianthus* in the Pinales; and *Helvetianthus* in an undefined order. *Rissikianthus* is distinctive amongst these genera in being the only form with typical pinalean scales bearing a pair of abaxial, horizontally aligned microsporangia. The three voltzialean genera all bear microsporangia attached to the scale stalk, while *Helvetianthus* is a very different strobilus without conventional scales or microsporangia.



Reconstructions
In the reconstructions of the four *Rissikianthus* species we attempt a faithful portrayal of the norm for each of the reference palaeodemes (from Pen 321, Aas 411, Umk 111 and Kap 111). Definite limitations have to be emphasised, however.

R. concavus (R3–4)—The Pen 321 palaeodeme shows excellent 3D (mould/cast) preservation in many specimens, such that the reconstruction is particularly reliable. The size and shape of the cones is remarkably constant, falling within a particularly narrow range of variation. This might be explained by their having occurred within a very limited area (<1 m along strike) of the thin chert bed in which they were found. They may even represent a single tree and a single season's growth. The microsporangia are in several instances clearly distinguished—in being notably delicate with a transparent bluish tinge in contrast to the more rusty brown woodiness of the cone scales.

R. linearis, *R. townrowii*, *R. convectus* (all R4)—The reference palaeodemes of these three species are far less clearly preserved. The outline shape of the scales, one of the diagnostic features in recognising species, are nowhere unambiguously seen in the available specimens.

Intactness & preservation of cones (Molteno)

The small *Rissikianthus* cones—as for their larger *Rissikistrobus* ovulate counterparts—are all preserved essentially intact. This holds for each of the five TCs in which they occur.

Microsporangia

It would appear that the normal condition of preservation of the Molteno *Rissikianthus* cones, in addition to being intact, is with their sac-like microsporangia in place. Each of the palaeodemes is briefly discussed:

Pen 321 Dic/Ris (30 indivs)—The microsporangia are best seen in the Pen 321 palaeodeme which has yielded a good number of mature cones from within a single closely confined pocket in the extensive cherty-mudstone horizon of Peninsula. These cones are exquisitely preserved as moulds/casts, mostly in longitudinal view, partly in section showing the delicate microsporangial sacs, partly in outer perspective showing clearly the shape of the scale face. Two cones [pl. 24(3, 4)] are preserved perfectly in cross-section displaying the microsporangia in plan view. Although all specimens from Pen 321 probably bear *in situ* microsporangia, they are particularly well seen in only seven of the 30 or so cones.

Aas 411 Dic/Sph (15 indivs)—Here the microsporangia are preserved as moulds/casts, much as at Pen 321, but occur in thinly laminated, strongly baked shale and are not as clearly seen. Most specimens show the axis and scales in longitudinal section and, in five of the 15 cones, *in situ* microsporangia are more or less clearly evident.

Umk 111 Dic 2 spp (8 indivs)—In contrast to Pen 321, and particularly Aas 411, the *Rissikianthus* cones from Umk 111 are preserved (as compressions in carbonaceous shale with potential cuticle) in outer view with the scales fully closed and overlapping. In two instances, the cones are seen largely in section showing (none too clearly) *in situ* microsporangia. As shown by Townrow (1967), the compression material from Umk 111 does yield cuticular material and *in situ* pollen.

Kap 111 Dic/Ris (25 indivs)—This relatively numerate palaeodeme derives from a thinly laminated, medium dark grey shale. The cones are seen partly in section, partly in outer view, but are not clearly preserved. The full pollen sacs are evident in some five instances.

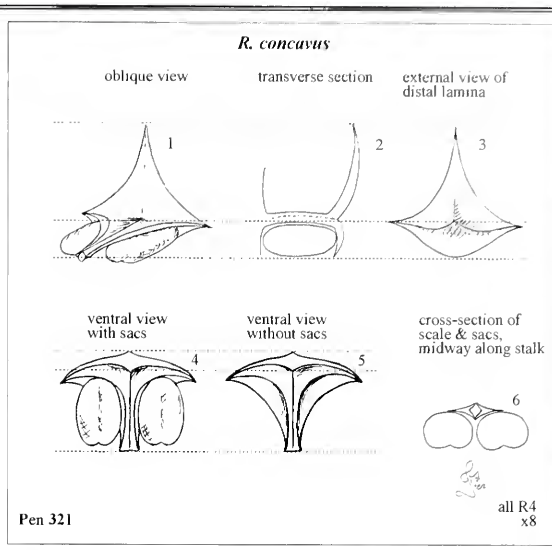
Boe 112 Dic cor (1 indiv)—The single specimen from this TC, though imperfectly preserved, shows *in situ* pollen sacs.

Cuticles (& *in situ* pollen)

Potential sample: Umk 111, 8 indivs.
Macerated (this work): nil.
Preservation grade: Grade 4–5.
Diagnostic characters: see Townrow (1967); this vol., p. 105.
In situ *pollen*: striate disaccate grains.
Comment: The grade and characters outlined above are based exclusively on Townrow (1967). We have not further studied the cuticle of the cones.
Significance:

Classification—The cuticle of *Rissikianthus* (and its affiliated organs) does not contribute unambiguously, in our knowledge, to classification within the Pinopsida in general or the Pinales in particular (but see Townrow's reflections quoted on p. 105).

Affiliations—Townrow (1967) established to his satisfaction that the cuticle of the affiliated organs (foliage and cones) corresponded. Some of his drawings are refigured on p. 105. For foliage cuticles, see p. 112.



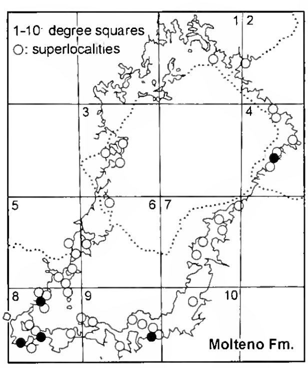
Adaptive radiation (Molteno diversity)

Assessment of diversity within *Rissikianthus* is particularly dependent on the clarity of preservation of the cones. Interpretation of critical diagnostic morphology is not always certain. Acknowledging the limitations, we find each of the four available palaeodemes (the single specimen from Boe 112 is not considered) to show nonoverlapping morphological variation and, therefore, to represent four separate species. It is in the shape of the scales (distal lamina), the number of scales per gyre and overall shape and size of the cones that the species are characterised.

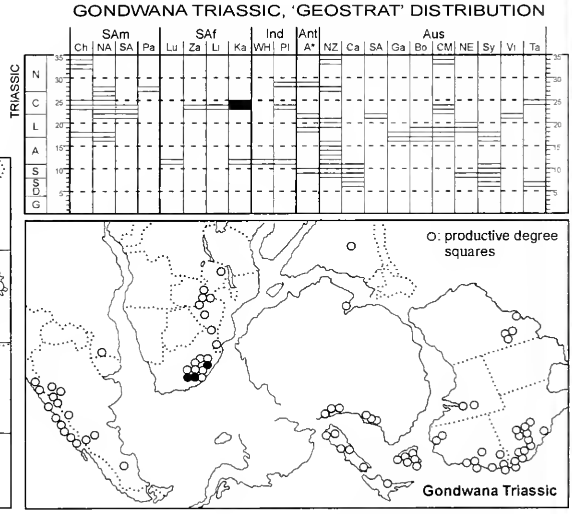
Should the diversity—of four species—be real, it is not reflected in the foliage where only a single variable species can be recognised in the four relevant TCs. Comparison of diversity with the affiliated female cones (*Rissikistrobus*) is complicated by the fact that only two well-represented, reasonably preserved palaeodemes (from Umk 111 and Aas 411) are at hand (Tab. 38). The collections from each of these sites, however, do indicate two distinctive species for both the male and female cones.

The four Molteno species are based on the TCs/reference palaeodemes as indicated below. Each derives from a distinct habitat and from a different level within the stratigraphic sequence—which lends support to the recognition of the four taxa.

R. concavus—Pen 321 Dic/Ris (Peninsula), 30 indivs
Dicroidium open woodland; Cycle 2f (Indwe Member)
R. linearis—Aas 411 Dic/Sph (Aasvoëlberg), 20 indivs
Sphenobaiera closed woodland; Cycle 1 (Bamboesberg Member)
R. townrowii—Umk 111 Dic 2spp (Umkomaas Valley), 8 indivs
Dicroidium riparian forest (mature); Cycle 2b (Indwe Member)
R. convectus—Kap 111 Dic/Ris (Kapokkraal), 25 indivs
Dicroidium riparian forest (immature); Cycle 2e (Indwe Member)



GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION



Rissikianthus concavus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/13674 a,b'x'; pls 23(2, 7, 8), 24(2).
Assemblage (TC): Pen 321 Dic/Ris; Peninsula.
Preservation: complete cone (missing proximal half of free axis), part and counterpart, longitudinal outer view and section with *in situ* microsporophylls; *ca* 60% flattened, exquisitely preserved; 3D mould and cast in thickly laminated, medium light grey shale with poor cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 30 indivs (intact strobili, partial strobili), pls 23(1–10), 24(1–4), 25(1–7).

Sister palaeodemes—nil.

Specific diagnosis
A *Rissikianthus* cone of small size and narrowly elliptic shape bearing *ca* 7 sharply concave-sided scales per gyre, and borne on a particularly long free gracile axis.

Specific characters
Strobilus: small (*ca* 10 x 3.4 mm), narrowly elliptical, apex acute, axis gracile, free axis particularly long (to 24 mm), scales *ca* 7 per gyre.
Microsporophyll: distal lamina with deep depression at insertion of stalk, commissure (line of junction) a very pronounced groove.

Etymology
concavus (Lat.)—with reference to the concave scale margin.

Comment & comparison
Of the four species of *Rissikianthus* recognised here, *R. concavus* is the most common and by far the most clearly preserved and distinctive. The reference palaeodeme of 30 individuals shows the cone exquisitely in outer view, longitudinal section and cross section.

Rissikianthus linearis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/20644 a,b; pl. 26(1–3).
Assemblage (TC): Aas 411 Dic/Sph; Aasvoëlberg.
Preservation: complete cone (missing proximal end of free axis), part and counterpart, longitudinal section, without microsporangia; impression in thinly laminated, strongly baked, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 15 indivs (intact strobili, partial strobili), pl. 26(1–9).

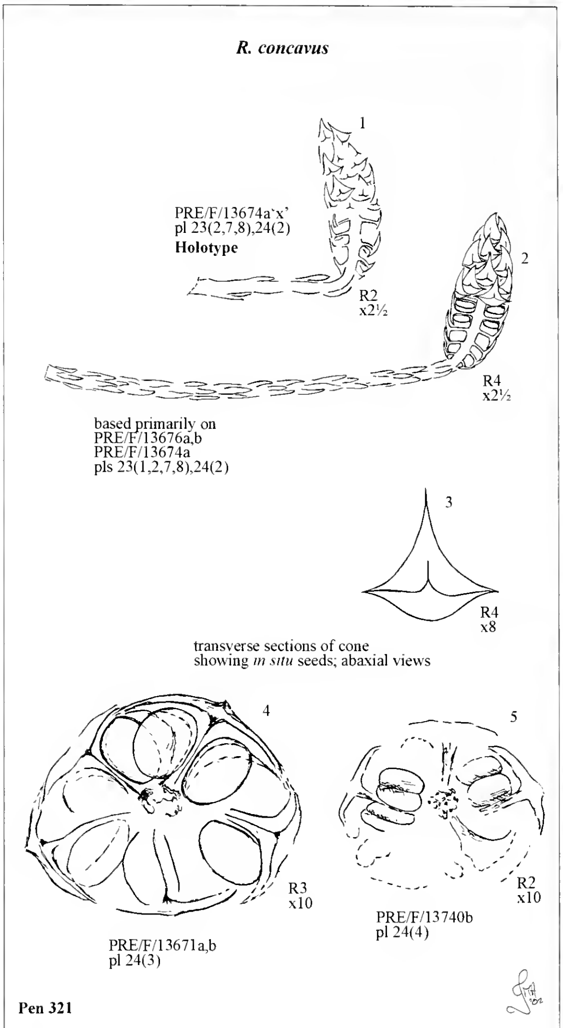
Sister palaeodemes—nil.

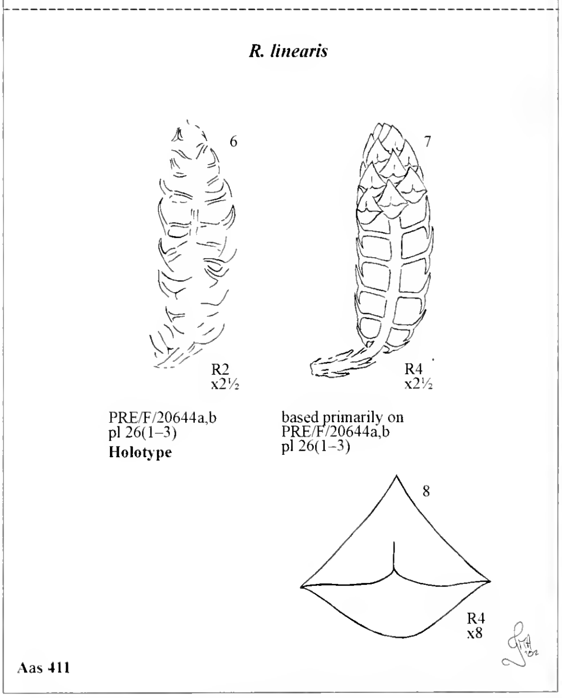
Specific diagnosis
A *Rissikianthus* cone of relatively large size and oblong elliptic shape bearing *ca* 6 weakly concave-sided scales per gyre, and borne on a short gracile free axis.

Specific characters
Strobilus: relatively large (*ca* 14 x 4.4 mm), oblong elliptical, apex obtuse, axis gracile, free axis medium, scales *ca* 6 per gyre.
Microsporophyll: distal lamina glabrous, outer margins straight to weakly convex, with moderate depression at insertion of stalk, commissure (line of junction) a clear linear groove.

Etymology
linearis (Lat.)—with reference to the linear shape of the strobilus.

Comment & comparison
This species compares most closely with *R. concavus* in various diagnostic features and differs from it most evidently in size and length of free axis. It is interesting that the four *Rissikianthus* species each represent a different habitat within the Molteno plain (Tab. 38) and that *R. linearis* and *R. concavus* occurred in woodland rather than forest.





Rissikianthus townrowii J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/6765a; pl. 27(7, 8).
Assemblage (TC): Umk 111 Dic 2spp, Umkomaas Valley.
Preservation: complete cone, primarily in longitudinal section, with microsporangia *in situ*; compression in thinly laminated, carbonaceous (good cuticle) moderately baked, dark grey shale with good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 8 indivs (mostly complete intact strobili), compressions with cuticle; pl. 27(1–8).

Sister palaeodemes—nil.

Specific diagnosis
A *Rissikianthus* cone of relatively large size and roundly elliptic shape bearing *ca* 12 finely striate, straight-sided scales per gyre, and borne on a short stout free axis.

Specific characters
Strobilus: relatively large (*ca* 14 x 7.4 mm), roundly elliptical, apex obtuse, axis robust, free axis short, scales *ca* 12 per gyre.
Microsporophyll: distal lamina finely striate throughout apical part, outer margins more or less straight, with shallow or no depression at insertion of stalk, commissure (line of junction) not pronounced.

Eponymy
townrowii—in honour of Dr John Townrow, who (in 1967) first described but did not name these male cones from the famous Umkomaas locality.

Comment & comparison
R. townrowii and *R. convectus* are similar in the nature and number of scales, but quite dissimilar to the other two *Rissikianthus* species. They occur within the mature and immature *Dicroidium* riparian forest habitats respectively (Tab. 38). *R. townrowii*, however, is distinct from *R. convectus* in the roundly elliptic shape of the strobilus and ornamentation of the exposed distal laminae of the scales.

Rissikianthus convectus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/16227; pl. 28(4, 5).
Assemblage (TC): Kap 111 Dic/Ris, Kapokkraal.
Preservation: complete cone (missing free axis), without counterpart, longitudinal section, without microsporangia; impression in thinly laminated, moderately baked, medium dark grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 25 indivs (intact strobili, partial strobili), pl. 28(1–7).

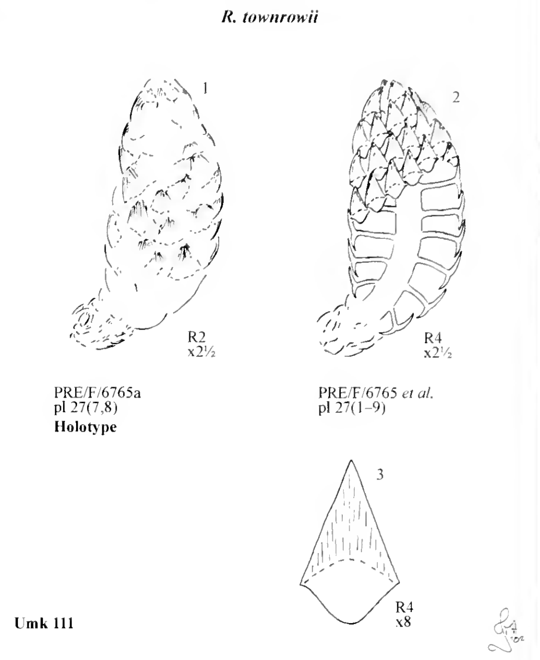
Sister palaeodemes—nil.

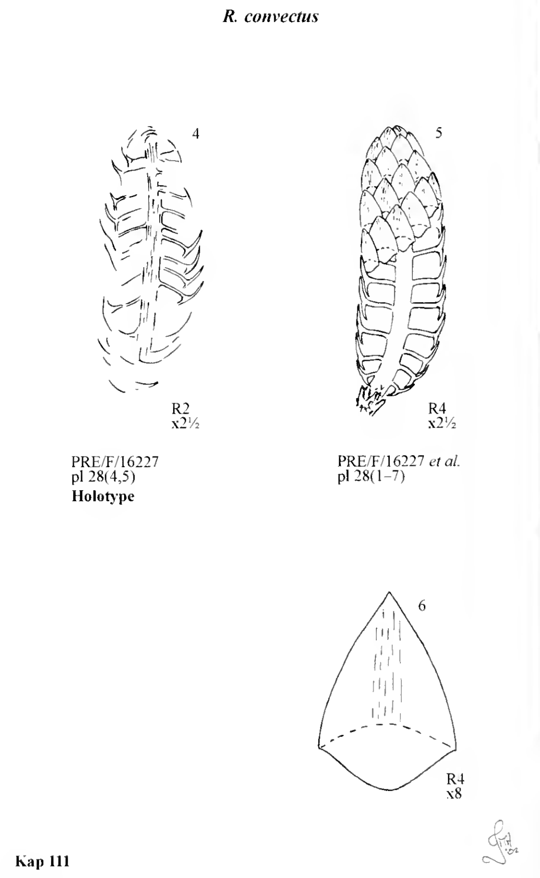
Specific diagnosis
A *Rissikianthus* cone of relatively large size and narrowly elliptic shape bearing *ca* 10 partially striate, convex-sided scales per gyre, and borne on a short moderately stout free axis.

Specific characters
Strobilus: relatively large (*ca* 17 x 4.4 mm), narrowly elliptical, apex obtuse, axis moderately robust, free axis short, scales *ca* 10 per gyre.
Microsporophyll: distal lamina finely striate down middle, outer margins convex, with shallow or no depression at insertion of stalk, commissure (line of junction) not pronounced.

Etymology
convectus (Lat.)—with reference to the convex scale margin.

Comment & comparison
R. convectus (from Kap 111), as noted above, is most like *R. townrowii* (Umk 111), the other species occurring in *Dicroidium* riparian forest, and is markedly distinct from the two woodland species. It differs from the Umk 111 species most notably in the linearly elliptical shape of the strobilus and the more restricted striated ornamentation on the scale face.





Rissikia Townrow 1967

Type species

Rissikia media (Ten.-Woods 1883) Townrow 1967.
Queensland, Australia; U. Triassic.

Generic diagnosis

A pinalean short shoot with linear single-veined leaflets that are helically attached and twisted near their base giving an overall appearance of a planar pinnate leaf.

Generic characters

Attachment: unknown.
Foliage shoot: short shoot individually dehisced, small, finely linear to elliptical; leaflets flattened, linear to narrowly elliptical, helically attached but twisted near base to extend in one plane on either side of rachis, adpressed to spreading at 80° from rachis, apex obtusely to acutely pointed, base clearly contracted or not contracted; with a single median vein.

Cuticle (adapted from And. & And. 1989); this vol., tfs 1–4 below.
Yield: Lit 111—15 specimens sampled, grade index 15/0/0/0/0.
Umk 111—19 specimens sampled, grade index 10/3/6/0/0.
Diagnostic characters (based on *R. media*, Umk 111)
Adaxial/abaxial: isobilateral, U & L cuticle of equal thickness.
Cell characteristics: narrowly oblong, end walls oblique to square; U & L cuticle with 450 cells per mm^2; walls straight to gently curved, profile triangular, plan gracile; cells over veins nondistinctive, noncutinised; occasionally faintly papillate.
Stomatal apparatus: haplocheilic, amphistomatic, U & L cuticle with *ca* 20 stomata per mm^2, nonaligned, longitudinal; subsidiary cells (anomo) brachyparacytic, 2 or 3 in number, noncutinised, radial walls normal; guard cells narrowly elliptic, 36 x 14 mμ, polar sulcus deep, non-ornamented, labia gracile; Florin ring lappetate, lappets flattened, arching; stomatal pit unknown.
Other features: none preserved.

Eponymy

Rissikia—after the family Rissik who, in the 1950s & 1960s, owned the land neighbouring that on which the Umkomaas locality (Umk 111) is sited.

Global range: 2 species, Gondwana, Tr. (ANI–NOR).
First: *Rissikia media* (Holmes 1982); Benolong, Dubbo, Australia.
Last: *Rissikia* (*Elatocladus raoi*) (Pal 1984); Tiki Fm., S. Rewa/Tiki, India.

Gondwana Triassic occurrence

Frequency (F): 17 degree squares (of the 84 across Gondwana).
Ubiquity (U): 5 continents (of 5 comprising Gondwana).
Diversity (D): 2 foliage species (as recognised in And. & And. 1989).
Abundance (A): 1% (the norm as in Molteno TCs).
Longevity (L): 14 myrs (late Anisian to early Norian).

Colonisation success: FUDAL rating 17/5/2/1/14 = 39.
Intermediate success (Grade 3): *Rissikia* was the 11th most prominent genus in the Gondwana Triassic; it was frequent, ubiquitous and fairly long-lived, but low in abundance and markedly lacking in diversity.
Endemism: of the two described Gondwana Triassic species, the rarer (*R. eskensis*) has a disjunct distribution (Karoo Basin, and Clarence-Moreton Basin, Australia), while the second (*R. media*) occurs scattered throughout the realm.

Molteno occurrence

Frequency (F): 21 TCs (of 100 sampled in the Molteno).
Diversity (D): 2 species.
Abundance (A): co-dominant (35–38%) in 2 TCs, occasional (1–2%) in 5 TCs, and <1% in the other 14 TCs.

Habit: probably a large tree.
Preferred habitat: *Dicroidium* riparian forest or *Dicroidium* open woodland, occasionally forming monodominant wetland stands.

Affiliated organs

Female strobilus: *Rissikistrobus*—Grade 4 (Kin. reinf., Mut. occ.).
Male strobilus: *Rissikianthus*—Grade 4 (Kin. reinf., Mut. occ.).

Classification & comparison (adapted from And. & And. 1989, p. 450)
Intergeneric comparisons

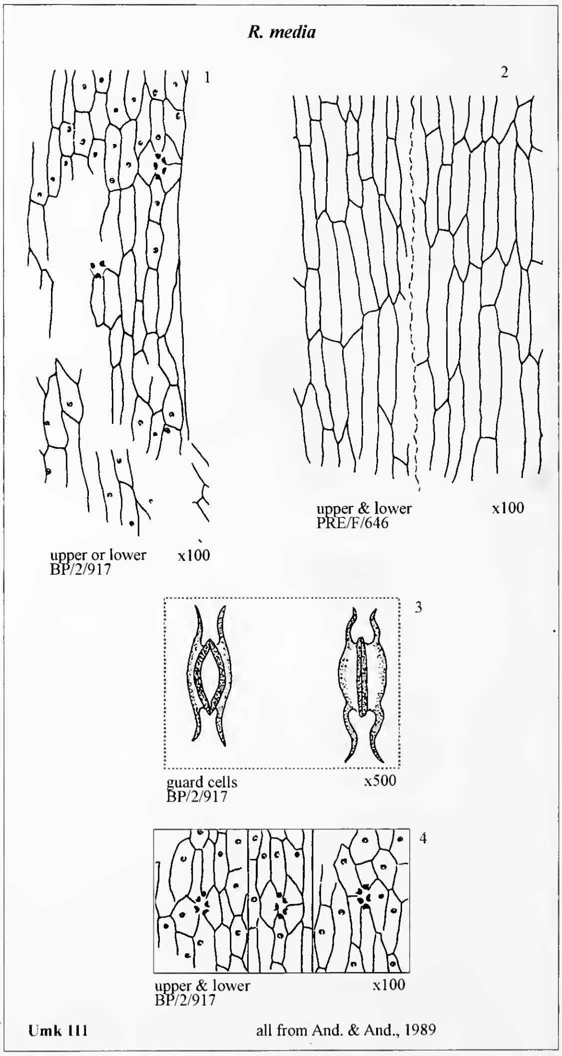
Gondwana Triassic pinopsid genera—The foliage of *Rissikia*, with its helically attached linear leaflets twisted near their base to spread in one plane, is quite distinct from that of the other four pinopsid genera found in Gondwana Triassic strata. *Voltziopsis* and *Pagiophyllum* leaflets are small, scale-like, distinctly thickened and unveined; while those of *Heidiphyllum* and *Clariphyllum* are relatively large, flattened and multiveined.

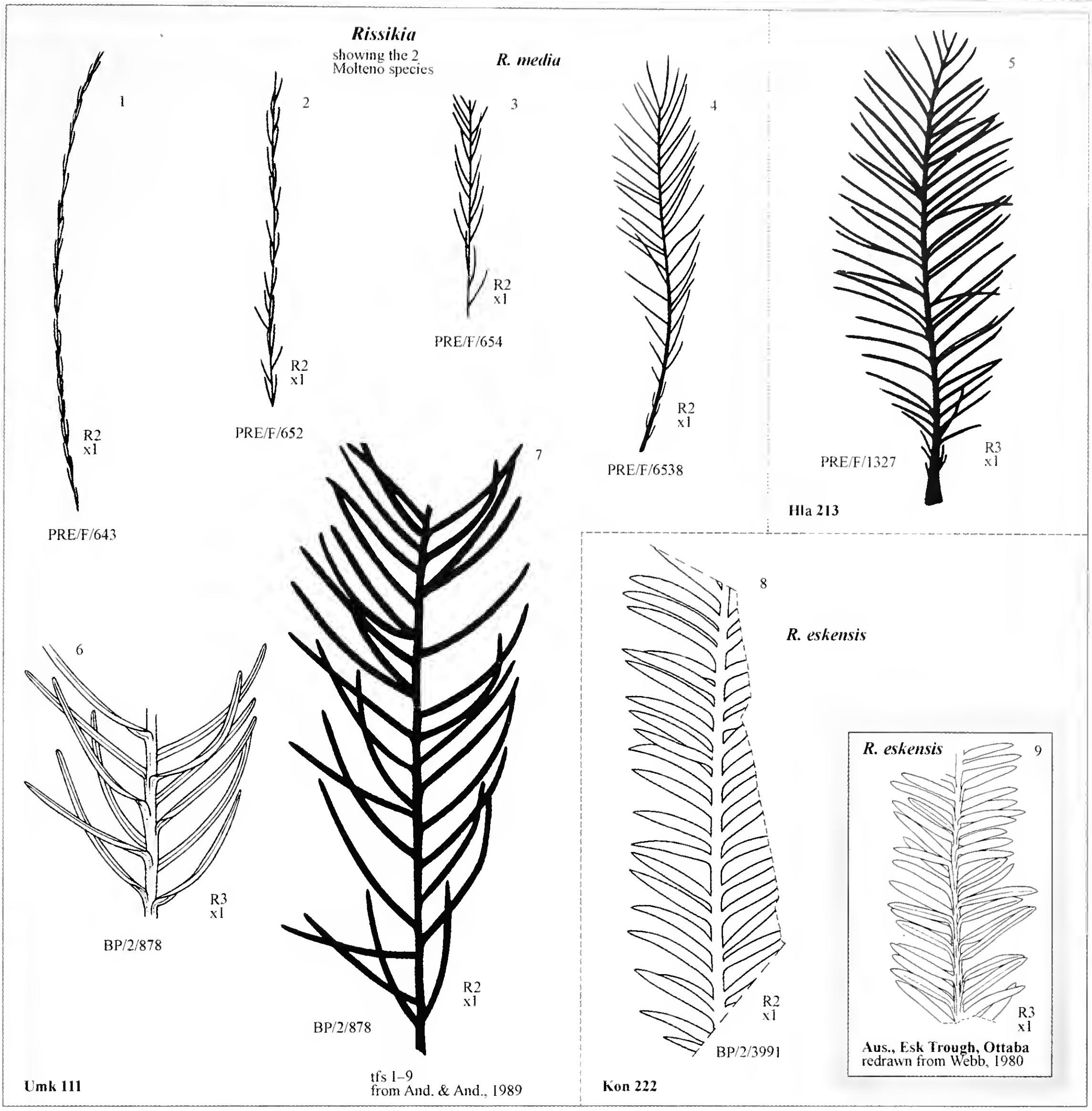
Other pinopsid genera—*Elactocladus* Halle (1913) is a global Mesozoic form-genus which is much like *Rissikia*. It differs principally in that its leaflets are spirally borne and strongly contracted at the base to form a short petiole attaching the leaf to a basal cushion.

Interspecific comparisons

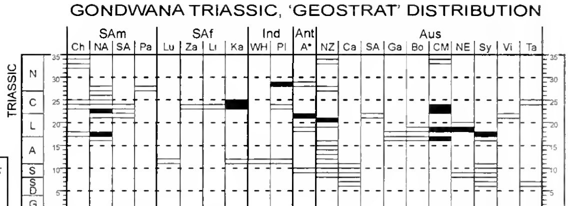
The two species of *Rissikia* recognised here from the Gondwana Triassic fall, on the basis of leaf macromorphology, readily within the compass of a natural genus. However, affiliated cones (female and male) and cuticle are known only for *R. media*, so it is not possible to confirm the true generic relationship between the two species.

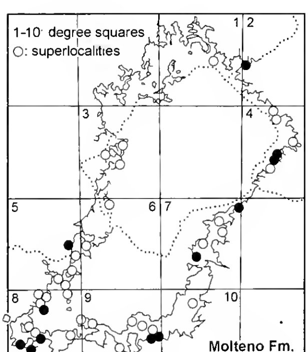
The reference palaeodemes of the two species are perfectly distinctive. A good number of additional palaeodemes, particularly from Australia, exist of both species and from the data at hand their appearance in the various assemblages appears to be virtually mutually exclusive. Resolving whether this is really true for the Australian material and whether the species are always distinct, must await more comprehensively published data.

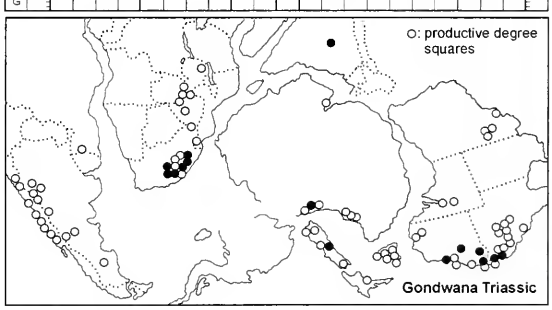


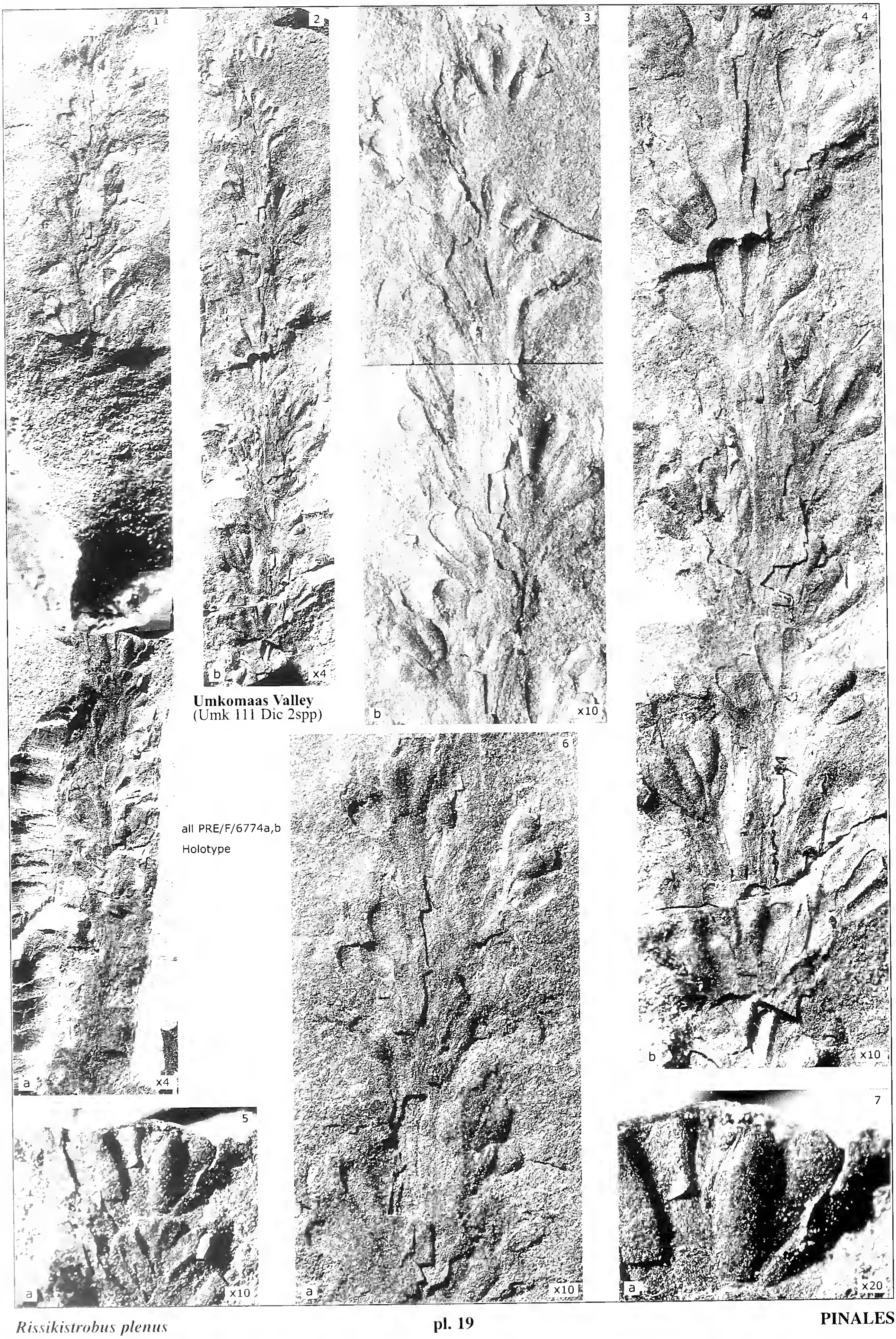


GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION

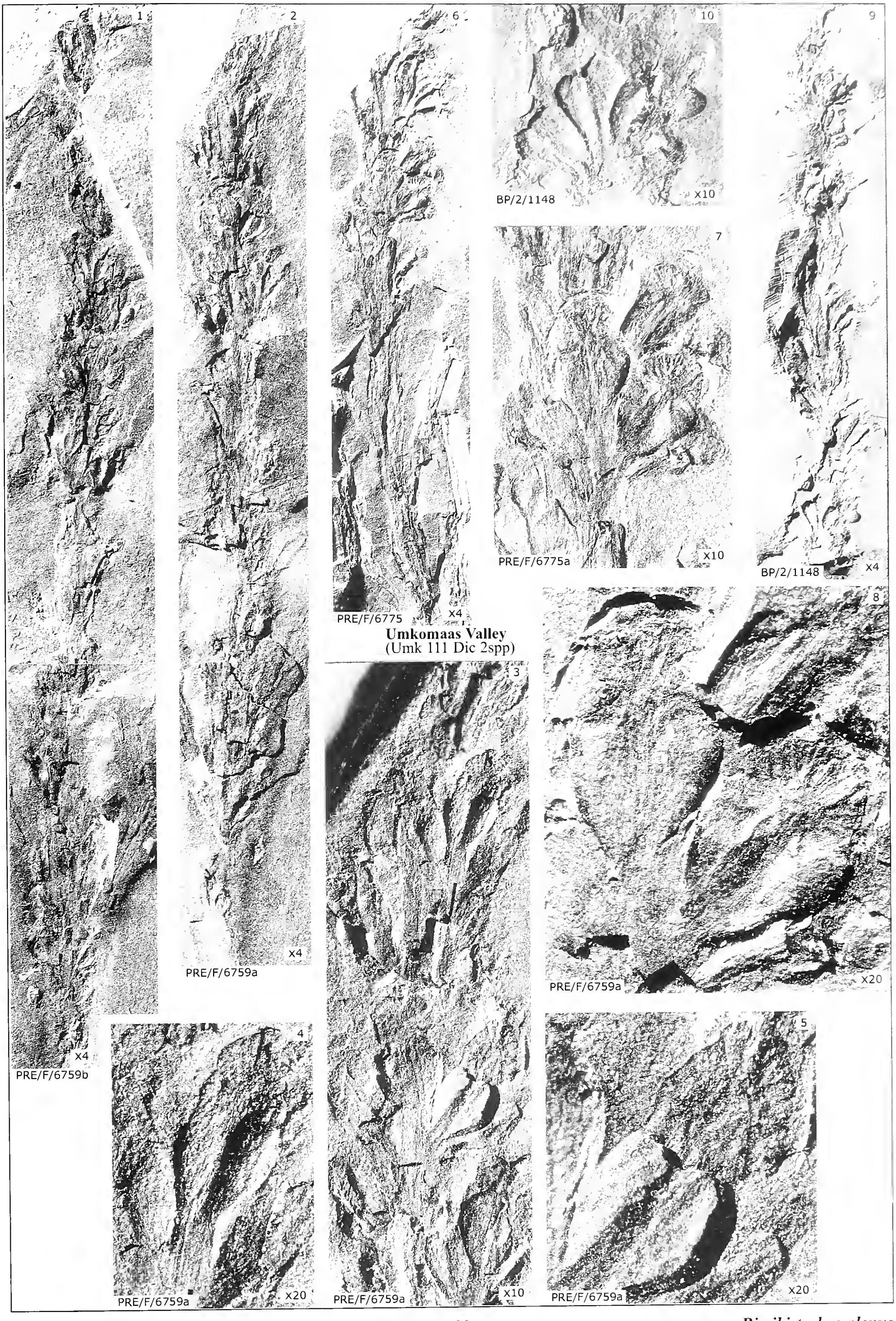




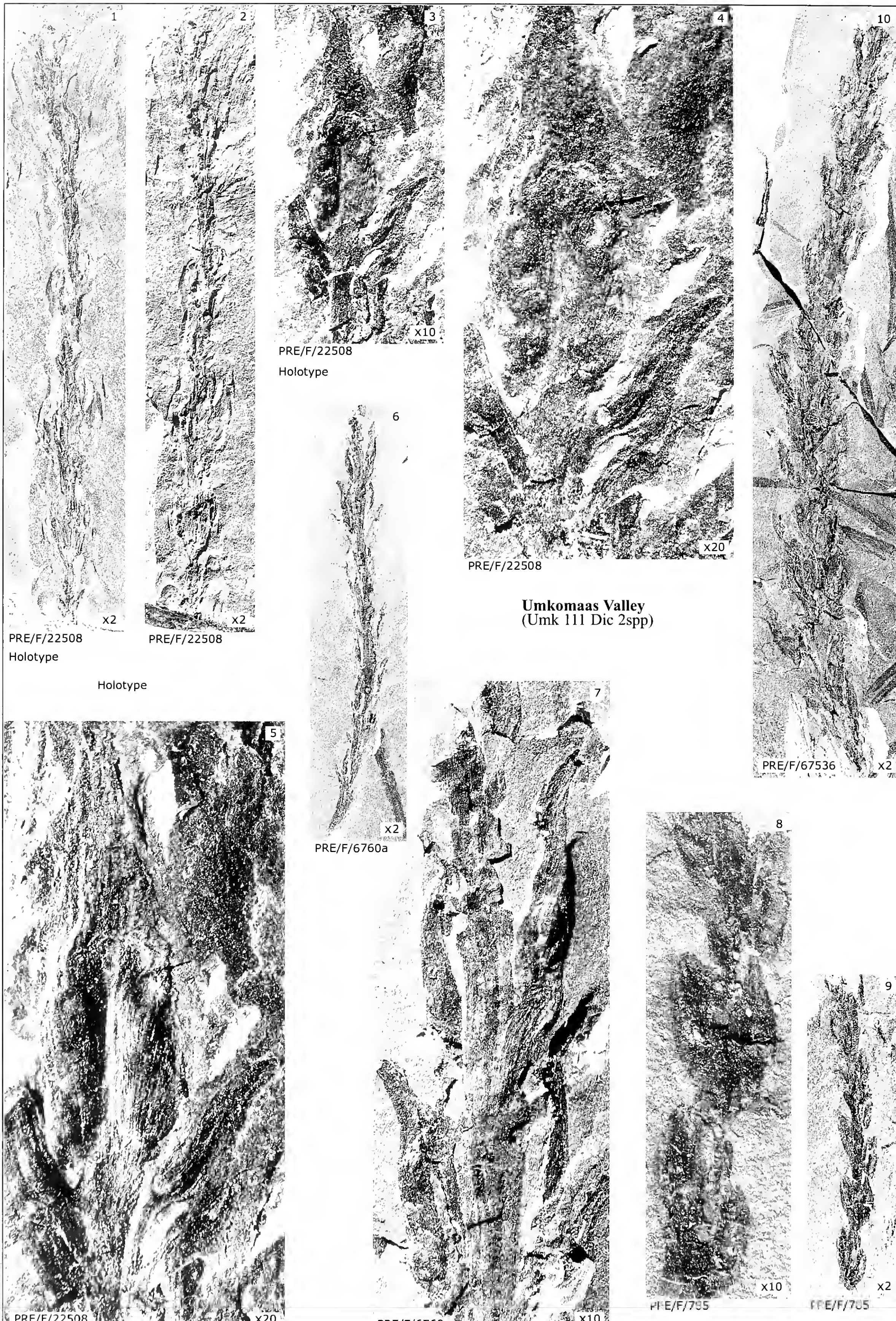




Rissikistrobus plenus pl. 19 PINALES



PINALES **pl. 20** ***Rissikistrobus plenus***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x2
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Holotype
2
x2
PRE/F/22508
Holotype
3
x10
PRE/F/22508
Holotype
4
x20
PRE/F/22508
Umkomaas Valley
(Umk 111 Dic 2spp)
10
PRE/F/67536
x2
6
x2
PRE/F/6760a
5
PRE/F/22508
x20
7
PRE/F/6760a
x10
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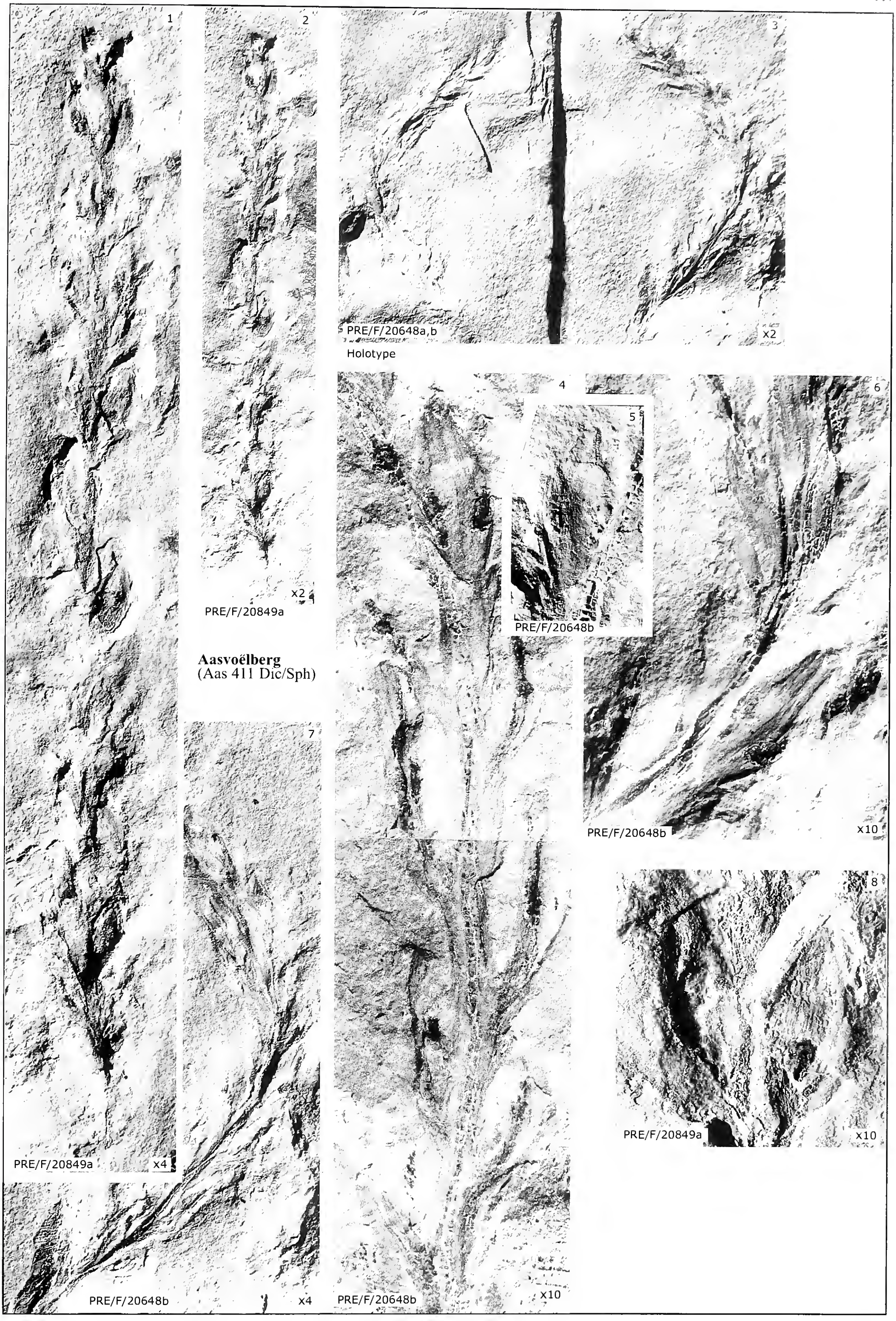
x2
PRE/F/785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PRE/F/20648b
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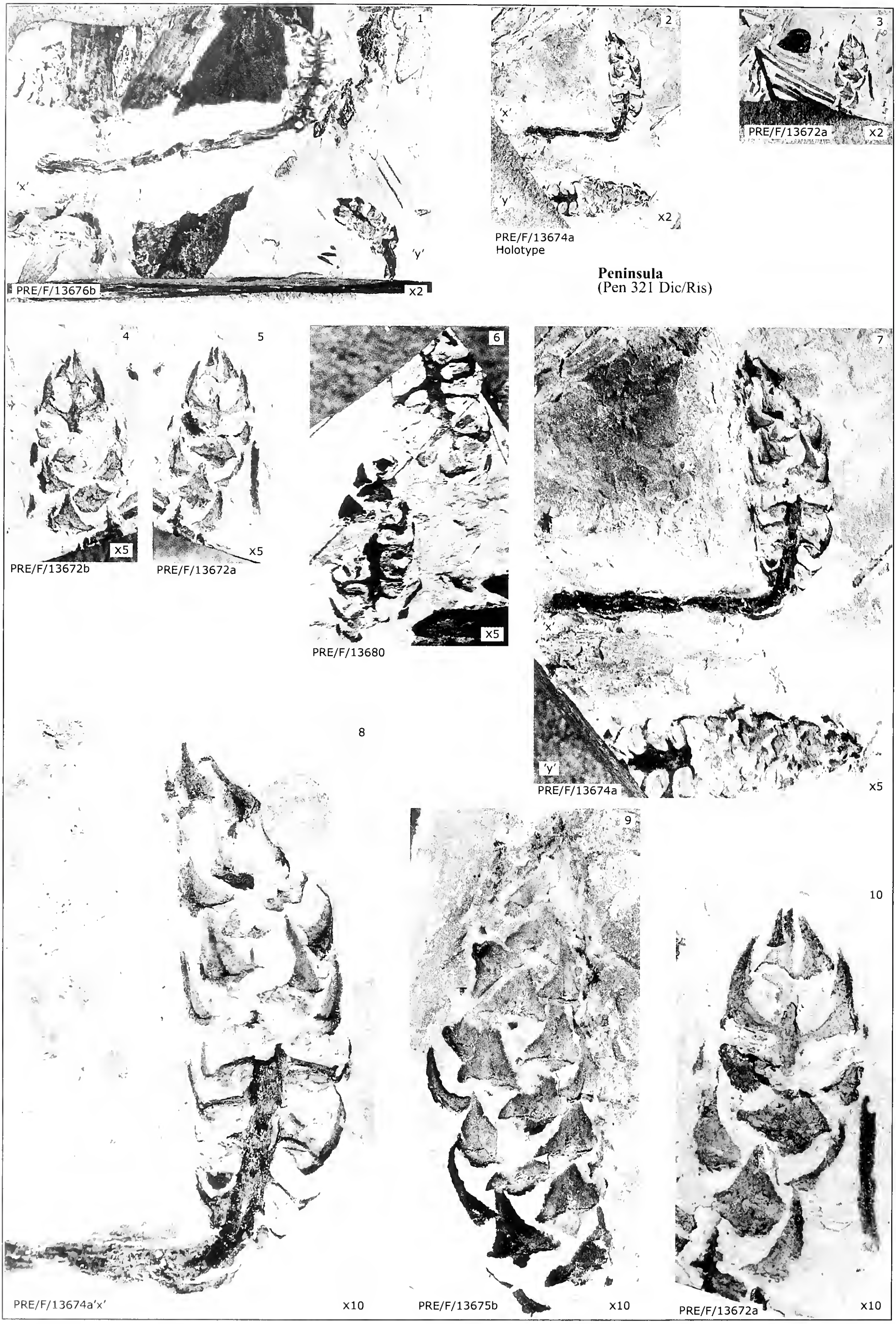
x4
PRE/F/20648b
x10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'y'
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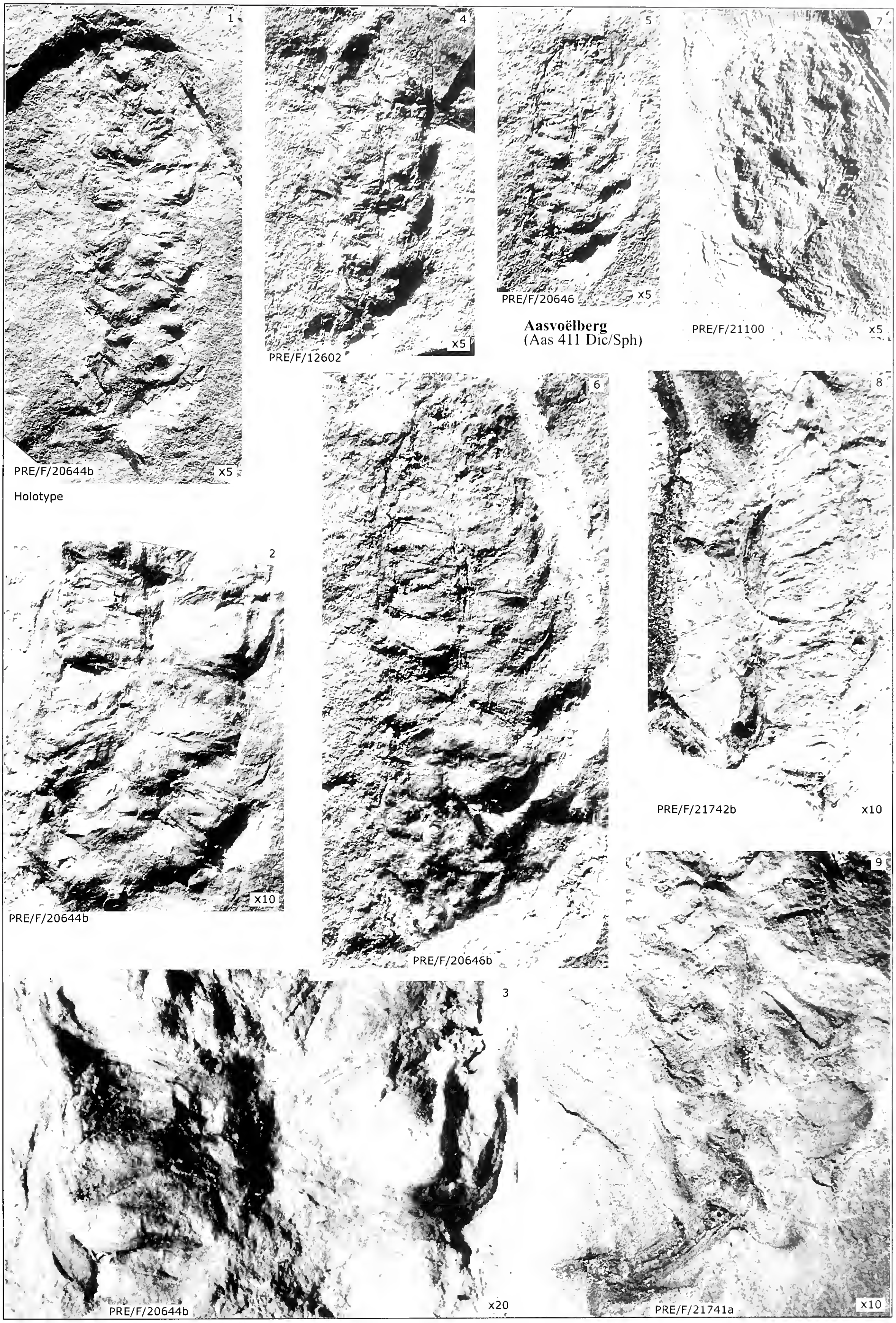
x2
2
'x'
'y'
x2
PRE/F/13674a
Holotype
3
PRE/F/13672a
x2
Peninsula
(Pen 321 Dic/Ris)
4
x5
PRE/F/13672b
5
x5
PRE/F/13672a
6
x5
PRE/F/13680
7
'x'
'y'
PRE/F/13674a
x5
8
PRE/F/13674a'x'
x10
9
PRE/F/13675b
x10
10
PRE/F/13672a
x10

Peninsula
(Pen 321 Dic/Ris)

Rissikianthus concavus **pl. 25** **PINALES**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x5
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(Aas 411 Dic/Sph)
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PRE/F/21100
x5
6
PRE/F/20646b
8
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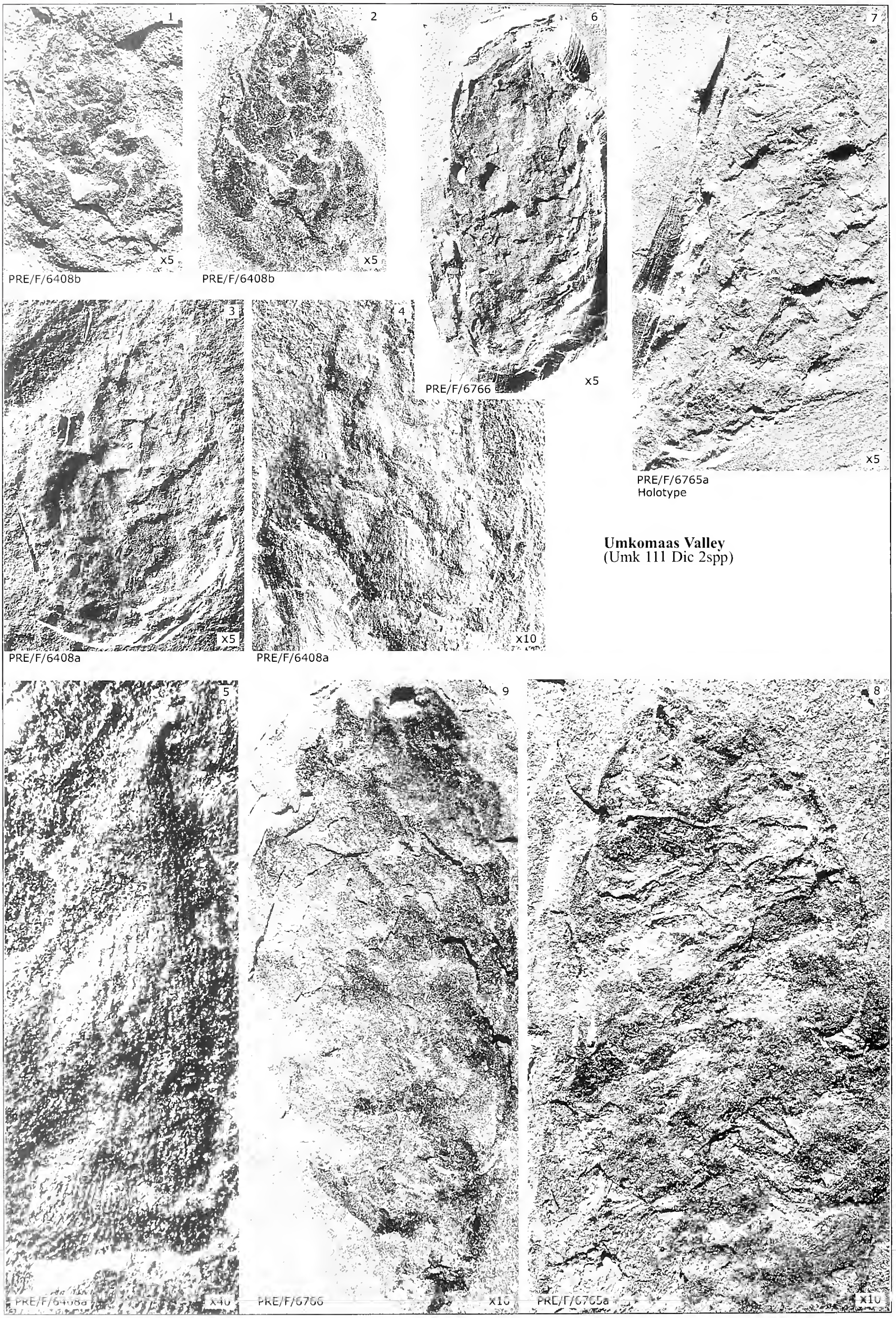
x10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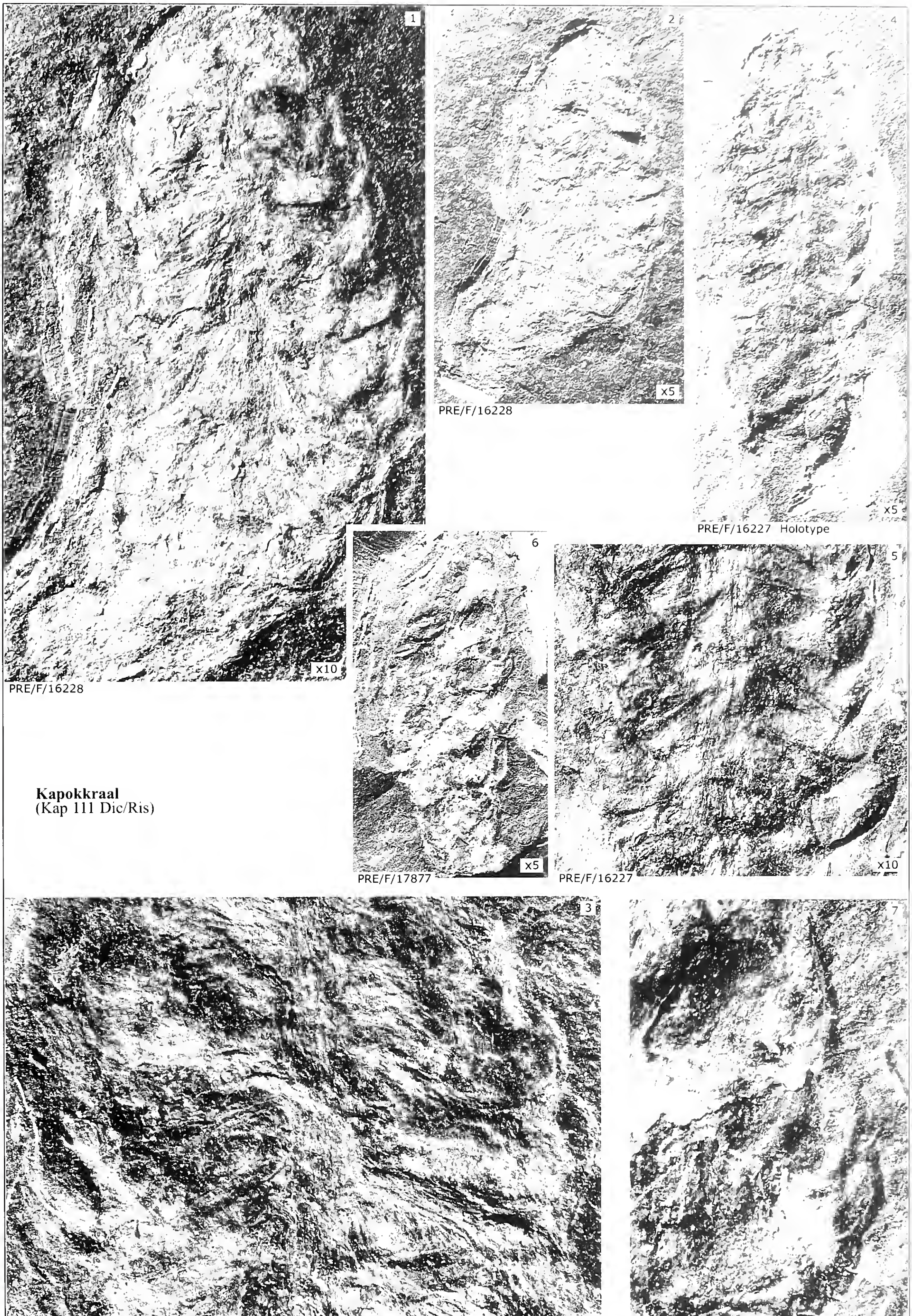
x5
PRE/F/6765a
Holotype
3
x5
PRE/F/6408a
4
x10
PRE/F/6408a
Umkomaas Valley
(Umk 111 Dic 2spp)
5
PRE/F/6408a
x40
9
PRE/F/6766
x10
8
PRE/F/6765a
x10


1
x10
PRE/F/16228
2
x5
PRE/F/16228
4
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PRE/F/16227 Holotype
6
x5
PRE/F/17877
5
x10
PRE/F/16227
Kapokkraal
(Kap 111 Dic/Ris)
3
x20
PRE/F/16228
7
x20
PRE/F/17877

PINOPSIDA S.V.Meyen 1984
PINALES S.V.Meyen 1984
INCERTAE SEDIS family

Pagiophyllum Heer 1881

Type species
Pagiophyllum circinicum (Saporta) Heer 1881.
Sierra de San Luiz, Portugal; U. Triassic (Malm).

Generic diagnosis: see Harris (1979).

Generic characters (after Harris 1979)
Foliage shoot: 'Shoot, bearing leaves in a helix; leaf about as broad as its basal cushion, length exceeding width of cushion. Blade not or scarcely narrowed at its base, in section broader horizontally than vertically'.
Cuticle: see And. & And. (1989, p. 465) for *P. bosei* (India) cuticle; this vol., tf. 3 below.

Etymology
Pagiophyllum—*pagio* (Gr.), firm, solid; *phyllum* (Gr.), leaf.

Global range: numerous spp., Pangaea-wide, Palaeozoic to recent.

Gondwana Triassic occurrence
Frequency (F): 4 degree squares (of the 84 across Gondwana).
Ubiquity (U): 4 continents (of 5 comprising Gondwana).
Diversity (D): 4 foliage species.
Abundance (A): <1% (the norm in Molteno TCs).
Longevity (L): 6 myrs.
Colonisation success: FUDAL rating 4/4/4/–/6 = 18.
Intermediate success (Grade 3): *Pagiophyllum* was the 12th most prominent genus in the Gondwana Triassic; it was of fairly low frequency, ubiquity, diversity, abundance and longevity. (Note that in Tab. 20 (p. 27), the hierarchical position is given as 21 and the FUDAL rating as 12. The reason for this is that the South American and Trans-Antarctic records were not yet included in the table.)
Endemism: all species are single-assemblage endemics.

Molteno occurrence
Frequency (F): 1 TC (of 100 sampled in the Molteno).
Diversity (D): 1 species.
Abundance (A): extremely rare at a single TC.
Habit: probably a tree.
Preferred habitat: possibly preferring *Sphenobaiera* open woodland.

Affiliated organs
Female strobilus: unknown.
Male strobilus: unknown.

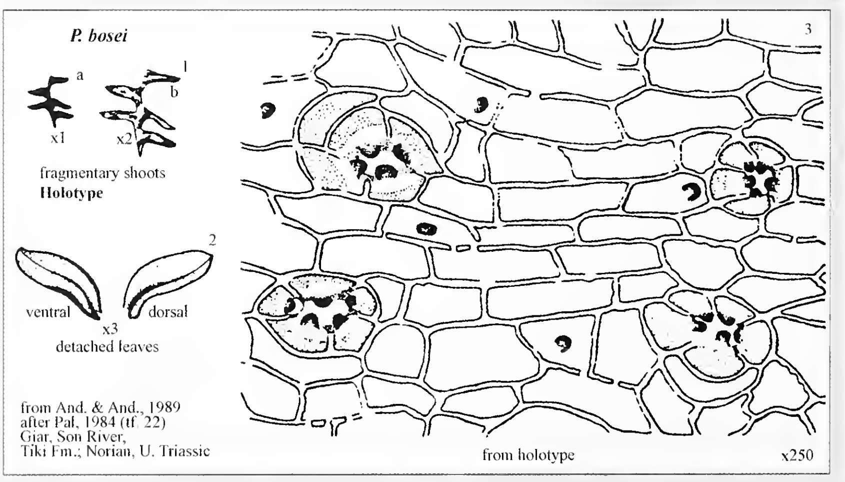
Classification & comparison (adapted from And. & And. 1989, p. 464)
Intergeneric comparisons
Gondwana Triassic pinopsid genera—Pagiophyllum is alone among the five pinopsid foliage genera (aside from *Clariphyllum*) found in the Gondwana Triassic in that it is a form-genus for which the cones remain unknown. The foliage shoots and leaflets are in many ways like those of *Voltziopsis*, but the cuticle of the latter is distinctly different (from the species *P. bosei*) in that its subsidiary cells are anomocytic to actinocytic, noncutinised and nonlappetate.

Other pinopsid genera—Brachyphyllum (Lindley & Hutton 1836) is a form-genus much confused with *Pagiophyllum*. It differs (after the diagnoses of Harris 1969, 1979) principally in that the free apical part of the leaflet is less than the width of the basal cushion, while in the latter it exceeds the width of the cushion.

Interspecific comparisons
As noted adjacent, *Pagiophyllum* is a pandemic form-genus incorporating numerous species from the Palaeozoic to recent. The foliage type is found associated with entirely different cones falling in widely separated conifer families such as the Cheirolepidiaceae and Taxodiaceae.

The two Gondwana Triassic species, including that now described from the Molteno, are extremely rare, being known only from their sparse reference palaeodemes—four illustrated individuals for *P. bosei* (India) and two individuals for *P. aasvoelense* (Molteno). [For more recent data on South American material, see Spalletti *et al.* (1991), and on Antarctic material, see Cantrill *et al.* (1995).]

Cuticle
The *Pagiophyllum* cuticle (based on the Indian species *P. bosei*) shows very different features from that of the other Molteno pinopsid genera. It has a thick cuticle with subsidiary cells that are regularly actinocytic, cutinised and strongly lappetate. *Dordrechtites*, *Heidiphyllum* and *Rissikia* (plus its reproductive affiliates) have thin cuticles with anomocytic or brachyparacytic subsidiary cells that are mostly nonlappetate. This would suggest that *Pagiophyllum* most probably falls in a position within pinopsid classification quite remote from the other Molteno genera.



Pagiophyllum aasvoelense J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/20820; pl. 29(3), tf.1 adjacent.
Assemblage (TC): Aas 411 Dic/Sph; Aasvoëlberg.
Preservation: impression in thinly laminated, strongly baked, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 2 individuals.

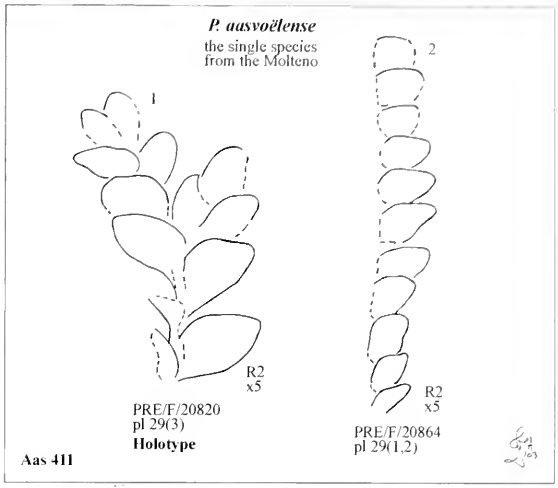
Sister palaeodemes—nil.

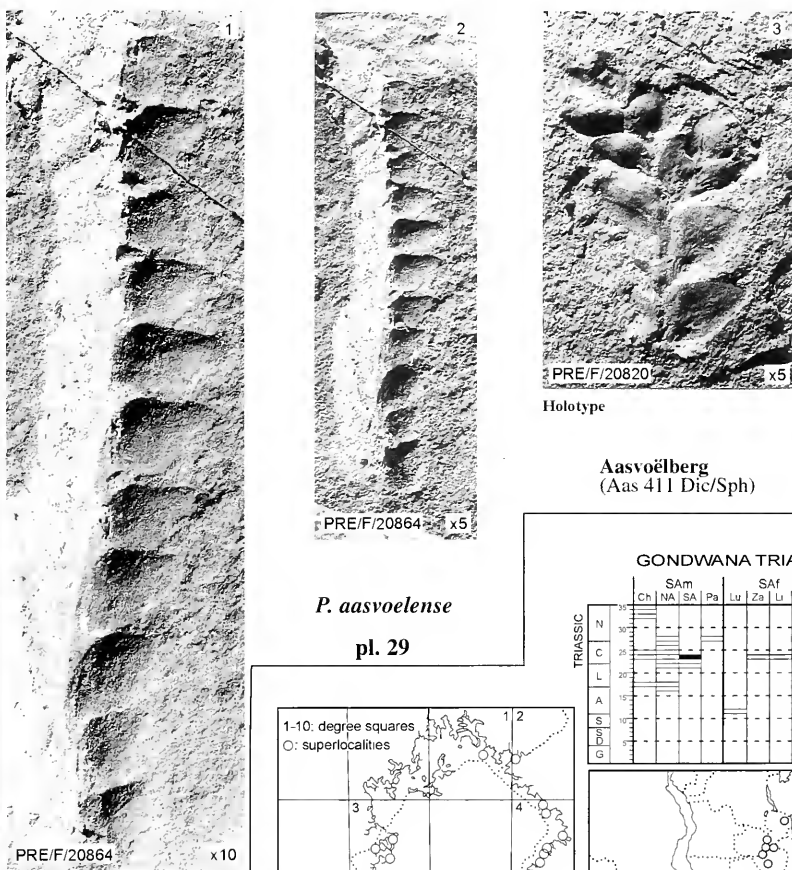
Specific diagnosis
A *Pagiophyllum* species with small (*ca* 2 x 0.1 mm) rhomboid to triangular leaflets.

Specific characters
Stem: *ca* 0.44 mm wide.
Leaf blade: rhomboid to triangular in shape, size varies from leaves 2 mm long in holotype to much smaller, 1 mm long, in the second individual. The attachment appears to be helical, with the leaves spread sideways.

Etymology
aasvoelense—after the type locality.

Comment & comparison
This species is similar to *P. bosei* (tfs 1–3 opposite) from India but the leaves are not strongly keeled. *P. papillatus* from Antarctica has leaves clearly helical, lanceolate and much larger (1–5 x 1–3 mm).



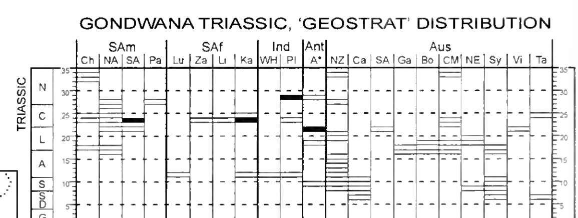


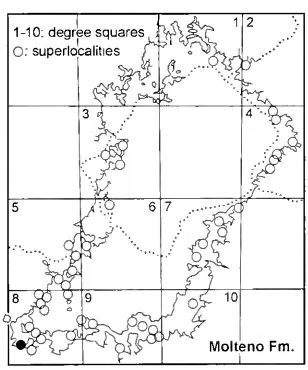
Holotype

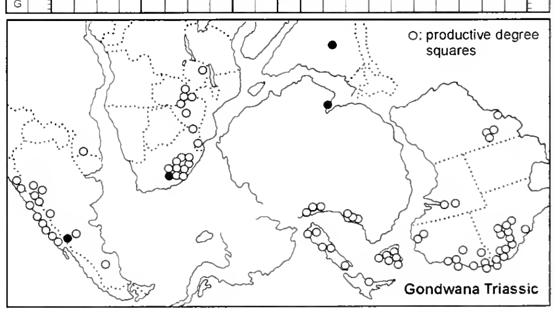
Aasvoëlberg
(Aas 411 Dic/Sph)

P. aasvoelense

pl. 29







PINOPSIDA S.V.Meyen 1984
INCERTAE SEDIS order
INCERTAE SEDIS family

Gypsistrobus J.M.And. & H.M.And., gen. nov.

Type species
Gypsistrobus scutatus J.M.And. & H.M.And., sp. nov.

Generic diagnosis
A pinopsid female cone of linear-elliptic shape with a gracile axis and single-lobed bract/scale complexes bearing single bilobed ovules.

Generic characters
Strobilus: cone compact, linear, small (to >35 x 6 mm); axis gracile (*ca* 0.8 mm diam.), free end *ca* 5–12 mm long, gently curving; megasporophylls spirally arranged, *ca* 6–8 units per gyre.
Megasporophyll: cone units consisting of ovuliferous bract/scale complexes; bracts free, leafy, lanceolate, *ca* 5 mm long; scales ovate, acute-tipped; ovules/seeds adaxial, single, bilobed, in concave surface of scale.
Ovule/seed: elongately oval, bilobed, 1–2 mm long.

Etymology
Gypsistrobus—gyps (Gr.), vulture, with reference to the type locality Aasvoëlberg, which means 'vulture mountain' in Afrikaans; *strobilos* (Gr.), cone.

Global range: 1 sp., Gondwana, Tr. (CRN).
First & last: the single Molteno species described here.

Gondwana Triassic occurrence
SAf—Karoo Basin, 1 TC (5 indivs).

Molteno occurrence
Frequency (F): 1 TC (of 100 sampled in the Molteno).
Diversity (D): 1 species.
Abundance (A): 5 individuals.
Aas 411 Dic/Sph: 5 indivs in 512 man-hrs cleaving (1 per 10 man-days), extr. rare

Affiliated organs
Female strobilus—unknown.
Foliage—unknown.

Within the pinopsid foliage and male-cone material preserved in the Aas 411 TC, there remain *Pagiophyllum*, *Fredianthus* and *Lutanthus* (*L. robustus*) without female-cone affiliates. These three genera appear to be most readily placed in the Pinales and Voltziales and are less likely to link with *Gypsistrobus*.

Classification & comparison
Suprageneric classification (family & order Incertae)

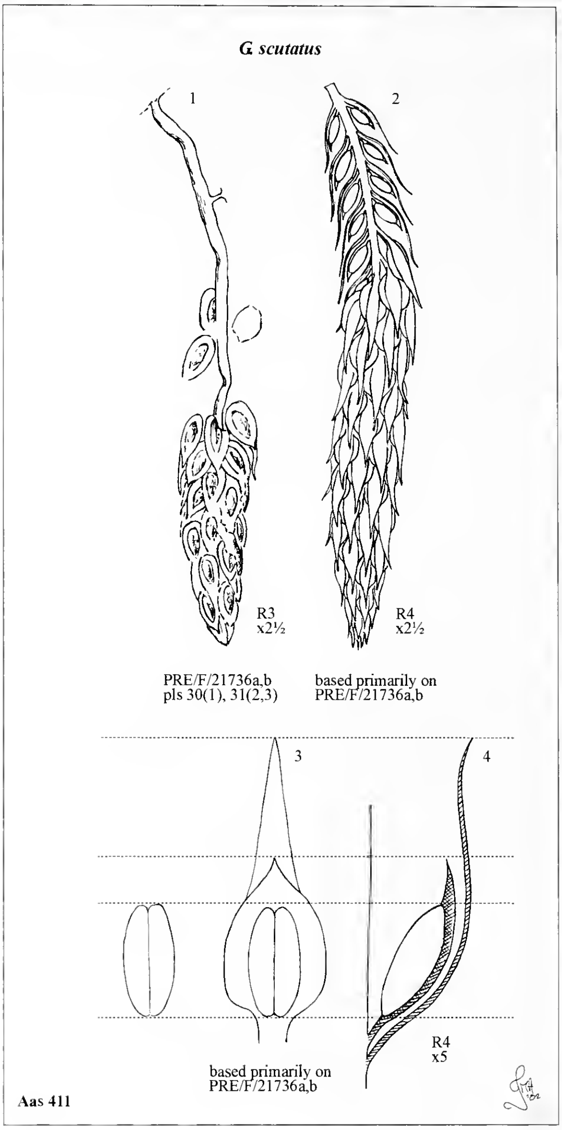
As for the following genus, *Avistrobus* (p. 130), we have made no attempt to include *Gypsistrobus* in our 'Global classification of the gymnosperms' (And. & And., in prep.). They most likely represent a single undescribed family and order of pinopsid.

The closest comparison would appear to be with *Ferugliocladus* (Ferugliocladaceae) of Archangelsky & Cuneo (1987) from the Permian (Asselian) Rio Genoa Group, Central Patagonian Basin, Argentina. This Permian genus bears megasporophylls with a large, triangular, free bract and single, sessile, orthotropous, fully enclosed ovules. We interpret the two Molteno genera as having naked ovules, but the material is insufficiently preserved to verify this.

Further somewhat similar ovulate genera are *Krylovia* and *Suchoviella* (order Cordaitanthales, family Rufloriaceae) from the Carboniferous–Permian of the former USSR. These genera both bear naked uni-ovulate scales superficially like *Gypsistrobus*, but with definite micropyles and no free bracts.

Intergeneric comparison (Gondwana Triassic)
Gypsistrobus is similar in size and shape of strobilus to *Rissikistrobus reductus* but differs in several respects: the ovules appear to be bifidly lobed rather than occurring in pairs; the megasporophylls dehisce readily and they show no evidence of persistent reduced foliage on the petiole.

Avistrobus, known only from a single specimen from Birds River (Bir 111), appears comparable to *Gypsistrobus* at family level. It differs most evidently in the scales bearing single ovules with no evidence of being longitudinally bilobed, and in the far more robust nature of the petiole and axis.



Reconstructions
The reconstructions are based on the holotype and two sister specimens of the reference palaeodeme (tfs 1–3 opposite).

In view of the imperfect preservation, the exact morphology of the bract/scale complex cannot be certainly established. Indeed, it is only in PRE/F/21736 (tfs 1, 2 above), interpreted as an immature cone, that the leafy bracts are seen. They appear to have been entirely lost in the four mature cones where the ovuliferous scales are seen in various states of disarticulation.

The cones are all shown in pendent orientation. The slender, seemingly herbaceous axes, could hardly have held these cones erect.

Gypsistrobus scutatus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/21090a,b; pls 30(3, 4, 8, 9), 31(1).
Assemblage (TC): Aas 411 Dic/Sph; Aasvoëlberg.
Preservation: fairly complete cone (apex and proximal end of axis missing), part and counterpart, longitudinal outer view with many scales; impression, imperfectly preserved; impression in thinly laminated, strongly baked, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 5 indivs (4 intact; 1 partial).

Sister palaeodemes—nil.

Specific diagnosis—as for genus.

Specific characters—as for genus.

Etymology
scutatus—*scutum* (Lat.), shield, with reference to the shape of the scale.

Classification & comparison—see notes for genus.

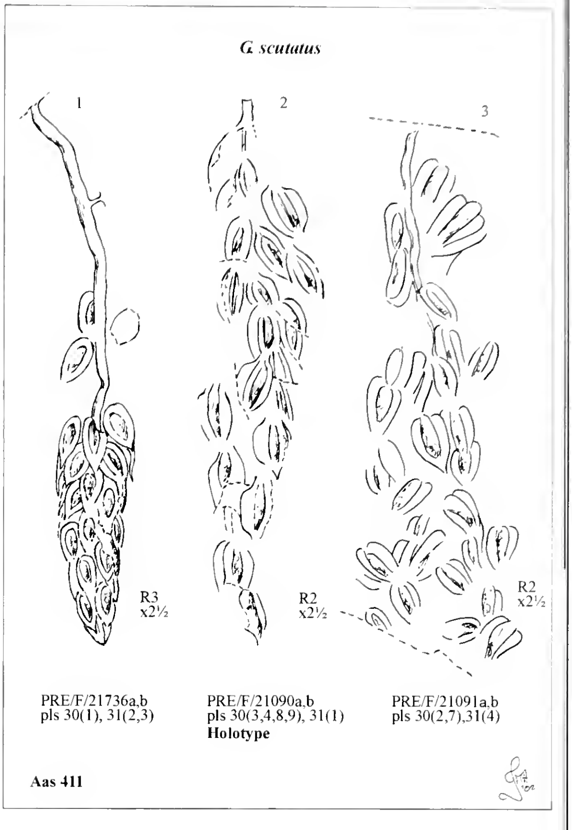
Intactness & preservation of cones
The five *G. scutatis* cones comprising the reference palaeodeme appear to represent a series showing progressive disarticulation.

PRE/F/21736a,b (tf. 1)—This we interpret to be an immature cone with fully intact scales along the distal half of the axis, with relatively small scales and only partially developed seeds, and with the bracts variously torn and shredded yet still in place. Were it not for this cone, we would have no knowledge of bracts characterising this taxon.

PRE/F 21090a,b (tf. 2)—The scales in this second cone are largely detached, yet still more or less in place, while the seeds are distinctly fuller and apparently mature.

PRE/F21091a,b (tf. 3)—This third figured specimen also appears mature, with full seeds and scales that presumably disarticulated to their relatively dispersed state after deposition.

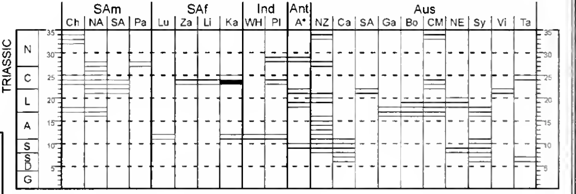
PRE/F/13099 & PRE/F/21328 (not figured as pen sketches)—The fourth and fifth specimens in the collection show similar or still further levels of disarticulation. PRE/F/13099 (not illustrated) is a more or less complete cone and set of scales in a state of post-deposition disarticulation much like that shown in tf. 2, while PRE/F/21328, pls 30(5, 6), 31(5, 6), is a cluster of scales dissociated from their parent cone.

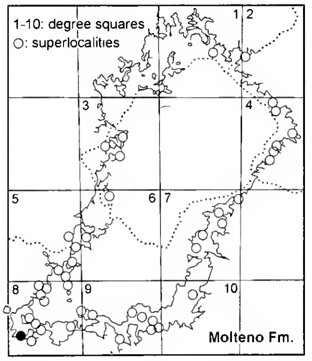


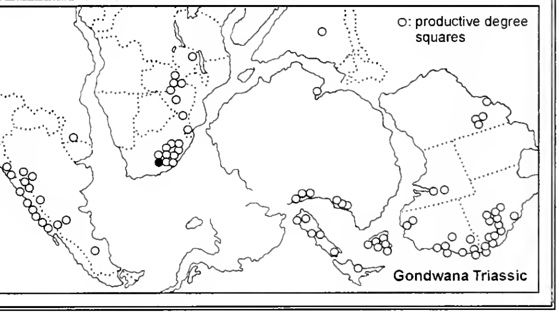
Molteno occurrence (elaborated)
For a full account of the Aas 411 TC, in which *Gypsistrobus* is unique, see And. & And. (in prep.) (a sequal to this work).

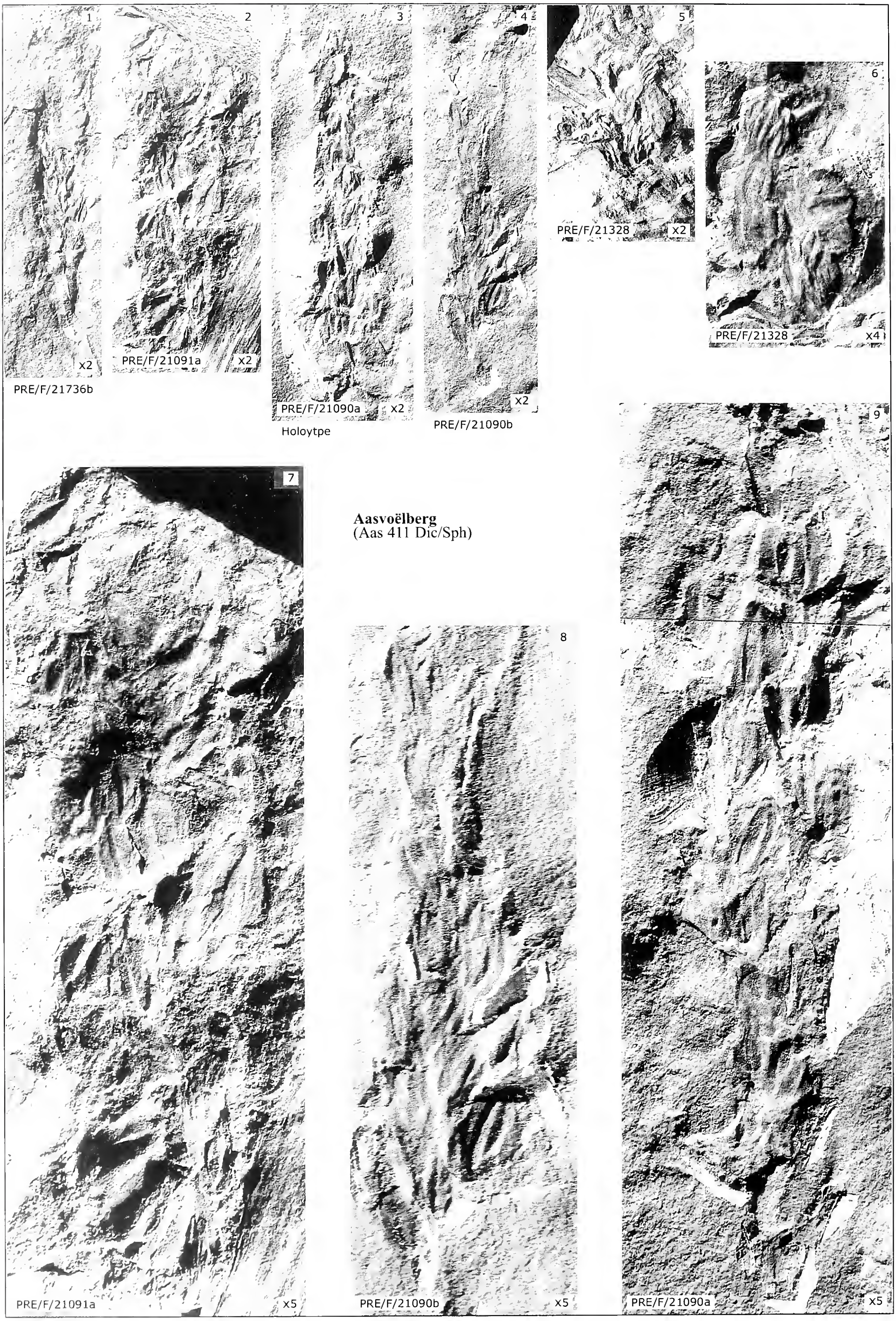
Habit & habitat
Given the rarity of *Gypsistrobus*, it is most likely an allochthonous element within the Aas 411 TC (a lake deposit in the floodplain). In the absence of foliage or male-cone affiliates, it is likely to represent a relatively rare element within the floodplain community.
The Aas 411 TC occurs low in the Molteno Fm. (Cycle 1) and appears to include a few possibly more primitive pinopsid taxa (e.g. *Fredianthus* and *Lutanthus robustus*) than the younger horizons.

GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION

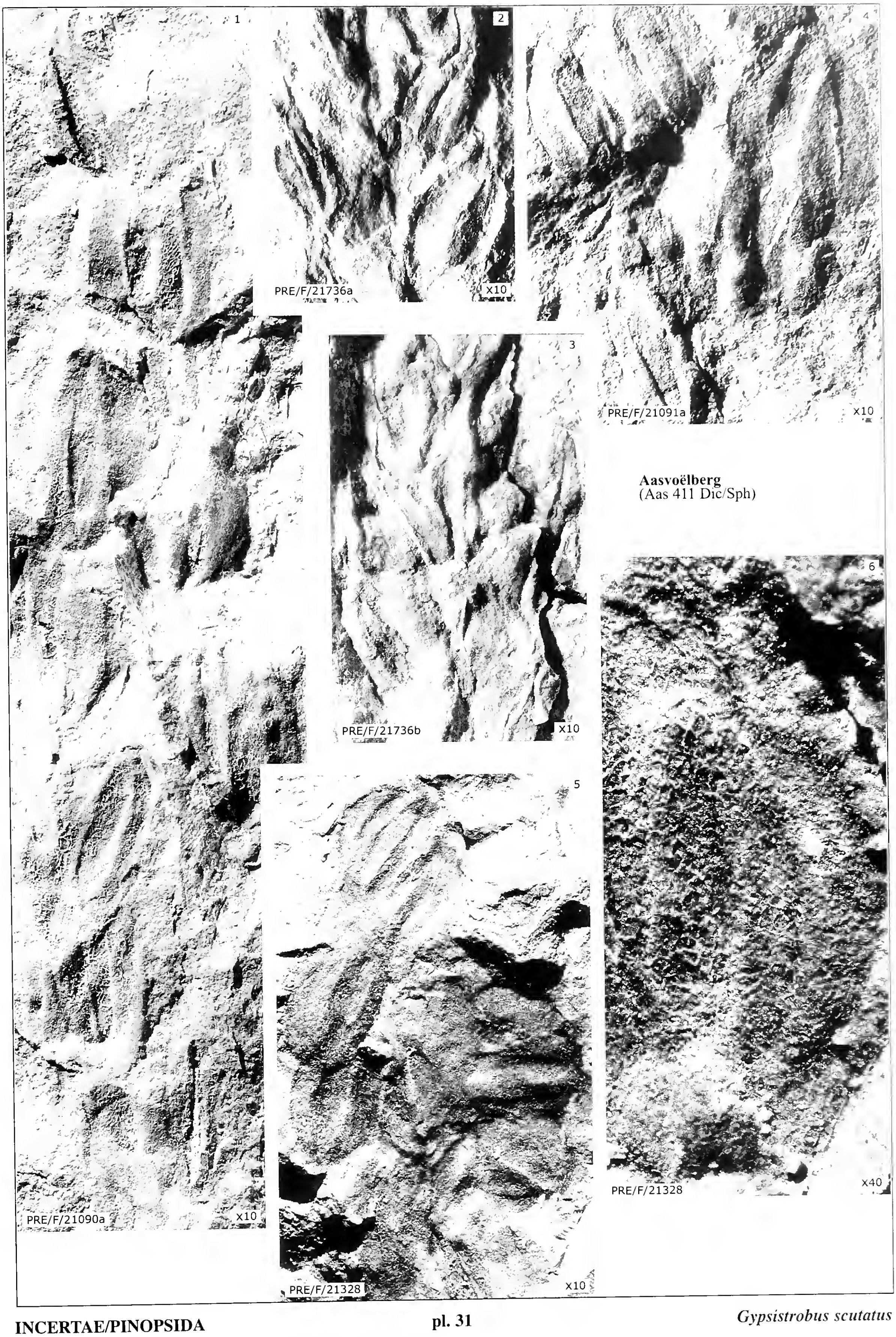








Aasvoëlberg
(Aas 411 Dic/Sph)



Aasvoëlberg
(Aas 411 Dic/Sph)

PINOPSIDA S.V.Meyen 1984
INCERTAE SEDIS order
INCERTAE SEDIS family

Avistrobus J.M.And. & H.M.And., gen. nov.

Type species
Avistrobus foliosus J.M.And. & H.M.And., sp. nov.

Generic diagnosis
A pinopsid female cone of elliptic shape with a stout axis and single-lobed bract/scale complexes bearing single unlobed ovules.

Generic characters
Strobilus: cone compact, oval, small (to >25 x 10 mm); axis robust (*ca* 1.5 mm diam.), gently curving; megasporophylls spirally arranged, *ca* 6–8 units per gyre.
Megasporophylls: cone units consisting of ovuliferous bract/scale complexes; bracts free, leafy, elliptical, *ca* 5 mm long; scales elliptical, acute tipped; ovules/seeds adaxial, single, in concave surface of scale.
Ovules: elliptical, with median rib, *ca* 1 mm long.

Etymology
Avistrobus—*avis* (Lat.), bird, with reference to the type locality Birds River; *strobilos* (Gr.), cone.

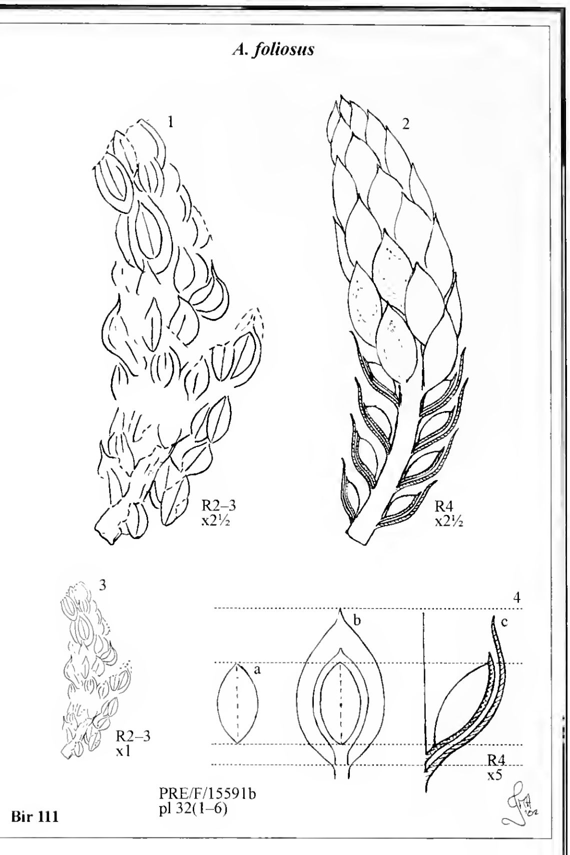
Global range: 1 sp., Gondwana, Tr. (CRN).
First & last: the single Molteno species described here.

Gondwana Triassic occurrence
SAf—Karoo Basin, 1 TC (1 indiv.).

Molteno occurrence
Frequency (F): 1 TC (1 indiv.).
Diversity (D): 1 species.
Abundance (A): 1 indiv.
Bir 111 2spp: 1 indiv. in 550 man-hrs cleaving (1 per 55 man-days), vanishingly rare

Affiliated organs
Female strobilus—unknown.
Foliage—unknown.

Classification & comparison
Suprageneric classification (family & order incertae)
For text relevant to both this and the previous genus, *Gypsistrobus*, see p. 126.
Intergeneric comparison (Gondwana Triassic)
Avistrobus, as noted previously (p. 126), has obvious similarities with *Gypsistrobus* from Aas 411. If both have been interpreted correctly, then they very likely represent the same family.
A second Molteno genus, *Switzianthus* (from Lit 111), is not dissimilar in size and shape of strobilus, but is known to be male through having yielded clear clusters of pollen grains. Cuticular comparison is excluded since the Bir 111 floral assemblage consists purely of impressions on buff shale.



Reconstruction
The reconstruction is based on the holotype (PRE/F/15591a, b), the only specimen found to date representing the taxon. Sufficient morphological detail is available to justify a sketch, though the bract/scale is certainly not securely interpreted.

Molteno occurrence (elaborated)
For an analysis of the Bir 111 TC, to which *Avistrobus* is exclusive, see And. & And. (in prep.), a sequel to the present work.
Habit & habitat
In view of its 'vanishingly rare' occurrence, *Avistrobus* is very likely an allochthonous element within the Bir 111 TC (a lake deposit in the floodplain). The plant was most probably a rare member of the floodplain community. It is of interest that *Avistrobus* (Bir 111) and *Gypsistrobus* (Aas 411) occur high and low in the Molteno sequence, respectively, in the only two thoroughly sampled lake-deposit TCs.

Avistrobus foliosus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/15591a,b., pl. 32(1–6).
Assemblage (TC): Bir 111 Sph 2spp; Birds River.
Preservation: virtually complete cone (proximal end of free axis missing), part and counterpart, longitudinal outer view with several scales seen from different perspectives; impression in thinly laminated, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage: as for holotype.
Specimens: the holotype.

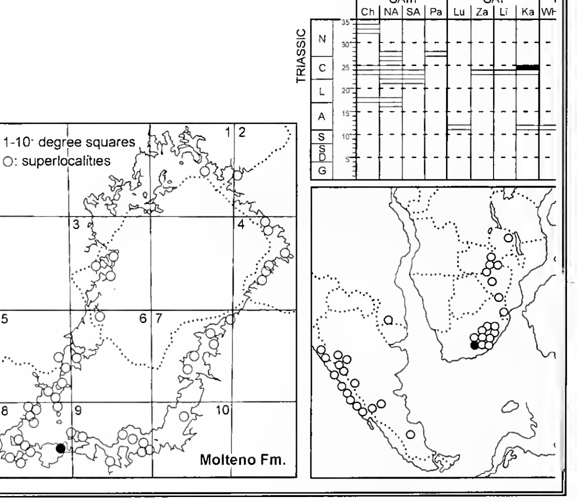
Sister palaeodemes—nil.

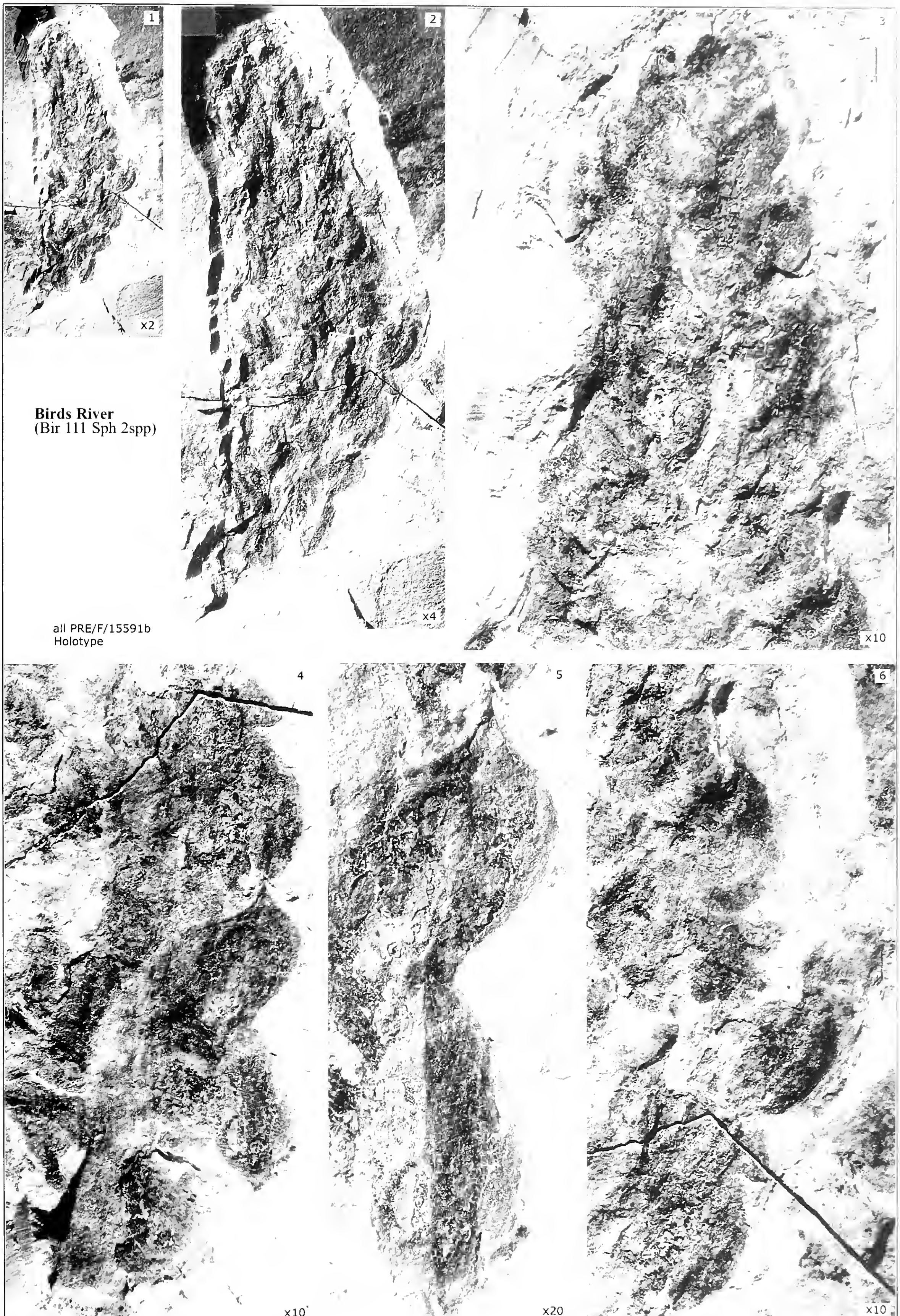
Specific diagnosis—as for genus.

Specific characters—as for genus.

Etymology
foliosus (Lat.)—leafy, with reference to the papery leaf-shaped bract.

Comments & comparison—see notes for genus.





INCERTAE/PINOPSIDA **pl. 32** *Avistrobus foliosus*

PINOPSIDA S.V.Meyen 1984
INCERTAE SEDIS order
INCERTAE SEDIS family

Helvetianthus J.M.And. & H.M.And., gen. nov.

Type species
Helvetianthus tintinnabulum J.M.And. & H.M.And., sp. nov.

Generic diagnosis
A putative pinopsid male cone with simple microsporophylls comprising single, sessile, spherical 4-lobed microsporangiate cupules.

Generic characters
Strobilus: simple, compact, spicate, small (20 x 9 mm); axis relatively stout (1 mm diam.), free end *ca* 3 mm, gently curved; microsporophylls spirally attached, sessile, 4 or 5 units per gyre.
Microsporophyll: spherical cupulate heads (*ca* 3 mm diam.), characteristically dehiscing along 4 clear suture lines into 4 lobes; leathery; surface ornamentation clear, isodiametric cells aligned and curving.
Microsporangium: no separate microsporangia observed.
Pollen: disaccate grains, *cf Alisporites*.

Etymology
Helvetianthus—after Little Switzerland, the type locality.

Global range: 1 sp., Gondwana, Tr. (CRN).
First & last: the single Molteno species described here.

Gondwana Triassic occurrence
SAf—Karoo Basin, 1 TC (6 indivs).

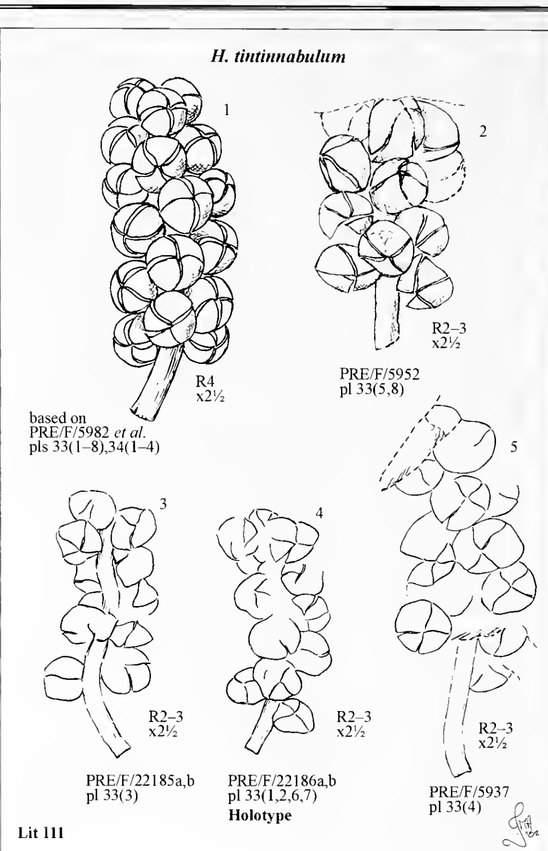
Molteno occurrence
Frequency (F): 1 TC (of 100 sampled in the Molteno).
Diversity (D): 1 species.
Abundance (A): 6 individuals total.
Lit 111: 6 indivs in 550 man-hrs cleaving (1 per *ca* 10 man-days), extremely rare

Affiliated organs
Female cone—unknown.
Foliage—unknown.

Classification & comparison
Suprageneric classification (family & order incertae)

Prior to isolating clusters of *in situ* pollen grains from one of the *H. tintinnabulum* specimens, we had taken the cupulate heads to be megasporophylls and had tentatively placed the strobilus in the Ginkgoopsida. As a compact male cone with spirally arranged microsporophylls, *Helvetianthus* appears closer to the Pinopsida or Cycadopsida. In the spherical, outwardly dehiscing nature of the pollen-bearing heads, however, the genus is very unlike any other male cone known to belong to either of these classes. In that the pollen grains are disaccate, a link with the Pinopsida or Ginkgoopsida is indicated. Overall, the evidence favours placement in the Pinopsida, but in a hitherto undefined order and family.

It is interesting to consider that in the angiosperm order Fagales, most notably in the families Myricaceae, Fagaceae and Casuarinaceae, the male and female flowers are characteristically distinct and cone-like. The casuarinas, in particular, have raised much debate amongst taxonomists as to their classification. Earlier workers were inclined to the opinion that they were the most primitive group of angiosperms and probably related to the gymnosperms, notably the Pinales and Ephedrales. Later botanists favoured the view that they were more advanced and that the peculiar features were extreme specialisations derived in isolation (Heywood 1993). Recent cladistic analyses incorporating molecular data (e.g. APG 1998; Nandi *et al.* 1998; Savolainen *et al.* 2000; Soltis *et al.* 2000) that have revealed considerable changes to our understanding of angiosperm phylogeny, support the latter view.



Reconstructions

The four R2–3 reconstructions cover the best of the six specimens of the reference palaeodeme. They are given the intermediate grade between R2 and R3 in that the four-lobed spherical heads are rather substantially reconstructed based on the best-preserved microsporangia in the set of available individuals.

The composite reconstruction (tf. 1 above) reflects the sum of features as seen in tfs 2–5 above. These allow a fairly confident reconstruction of the complete *Helvetianthus* cone.

Molteno occurrence (elaborated)

For an analysis of the Lit 111 TC, yielding the only known *Helvetianthus* specimens, see And. & And. (in prep.), a sequel to the present work.

Habit & habitat

Like the two previously described ovulate genera, *Gypsistrobus* and *Avistrobus*, which are unique to Aas 411 and Bir 111 respectively, *Helvetianthus* is unique to Lit 111. And like those two genera, its great rarity suggests that it is an allochthonous (possibly parautochthonous, considering the delicate nature of the strobilus) element in the deposit, formed in an abandoned marginal channel of a braided river with raised banks supporting dense *Dicroidium*-dominated riverine forest. In view of the nature of the well-preserved cuticle without stomata it is proposed that *Helvetianthus* was borne on an undershrub or herb of the *Dicroidium* forest.

Evidence for affiliation of organs

Of the seven genera of female fruit and 18 of foliage identified at Lit 111, none are evident candidates for linkage with *Helvetianthus*. While several of the foliage genera from the TC remain unpreoccupied, there is no persuasive evidence, from cuticle (And. & And. 1989) or otherwise, for affiliation. *Jeanjacquesia* and *Moltenia*, putative cycadalean fronds (see Tabs 6a, 13), cannot be excluded from possibility, nor can *Saportaea*, represented in the Molteno by only one large leaf from Lit 111. A further possibility is *Paraginkgo antarctica*, which is placed here in a new genus as the cuticle is unique and quite unlike that of other Molteno *Ginkgoites* species. Of the seven ovulate genera from Lit 111, two remain without proposed male counterparts: *Dordrechtites* and *Fraxinopsis* (Tab. 6b). They offer no clues for pairing with *Helvetianthus*.

Helvetianthus tintinnabulum J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/22186 a,b; pls 33(1, 2, 6, 7), 34(2).
Assemblage (TC): Lit 111 Dic/Hei; Little Switzerland.
Preservation: fairly complete strobilus (apical portion missing), part and counterpart, longitudinal outer view with several cupulate heads; compression in thinly laminated, carbonaceous (good cuticle) dark grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 6 individuals; 2 with counterparts, all are well preserved compressions with cuticle; together they allow the full cone to be reconstructed.

Sister palaeodemes—nil.

Specific diagnosis—as for genus.

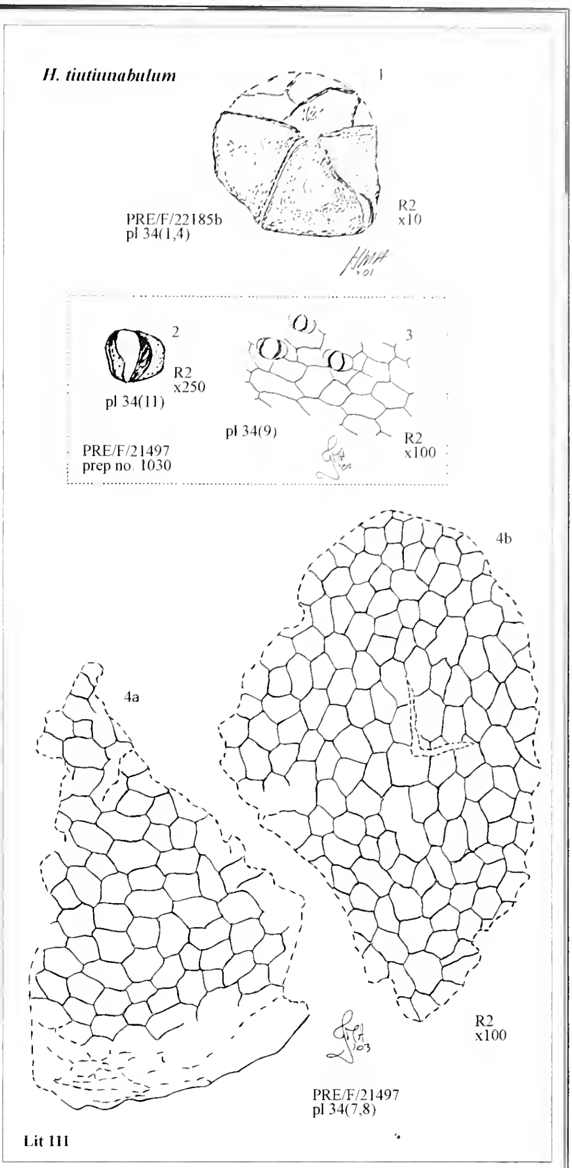
Specific characters—as for genus.

Etymology
tintinnabulum (Lat.)—a bell, with reference to the strobilus appearing like a string of bells.

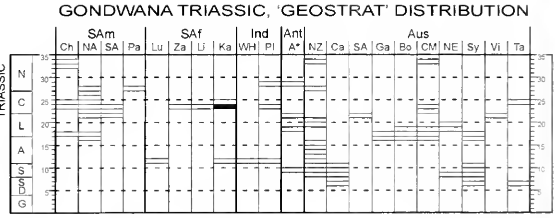
Classification & comparison: see notes for genus.

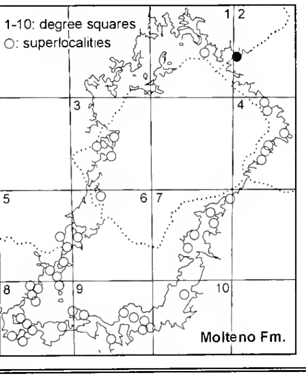
Intactness of cones
All six available cones are fully intact, with the fragile-appearing cupulate heads preserved essentially in place. Four of these are virtually complete, while the remaining two are missing the apical part of the cone.

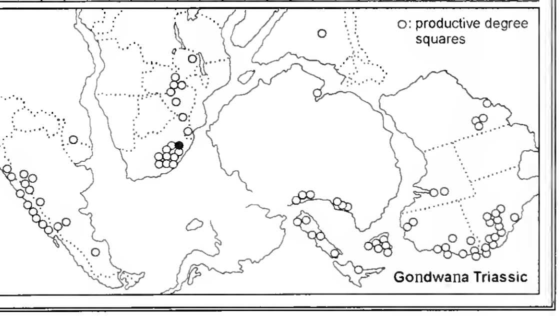
Cuticles (& *in situ* pollen)
Potential sample: Lit 111, 6 indivs.
Macerated (this work): Lit 111, cupulate heads from 5 indivs.
Preservation grade: Grade 5 (excellent), all features clear, large pieces.
Diagnostic characters: cells isodiametric, pentagonal-hexagonal, walls straight to gently curved; papillae single, bold, central; stomata absent; other features absent.
In situ *pollen*: disaccate grains, nonstriate; occur in aggregated masses; similar to pollen isolated from *Pteruchus* by Townrow (1962) and dispersed grains from Lit 111 identified as *Alisporites* in And. & And. (1983, pl. 30, figs 14–16).
Comment: the cuticular structure is visible on the surface of the microsporangia, even at low magnification (pl. 34, figs 1–6).
Significance:
Classification—The cuticle, in its thickness and cellular features, is most reminiscent of the ginkgoopsid genera (e.g. *Dicroidium*) which would suggest placing *Helvetianthus* in this class. The disaccate grains would tend to support this. In view of its (remotely) cone-like appearance, however, we have placed it in the pinopsids. *Helvetianthus* remains a phylogenetic enigma.
Affiliations—We have not proposed any likely affiliates for *Helvetianthus*. If the genus should prove to be ginkgoopsid, then it might conceivably affiliate with *Paraginkgo* (found most commonly at Lit 111) which remains without male or female counterparts. But the cuticle of these two genera does not corroborate this.

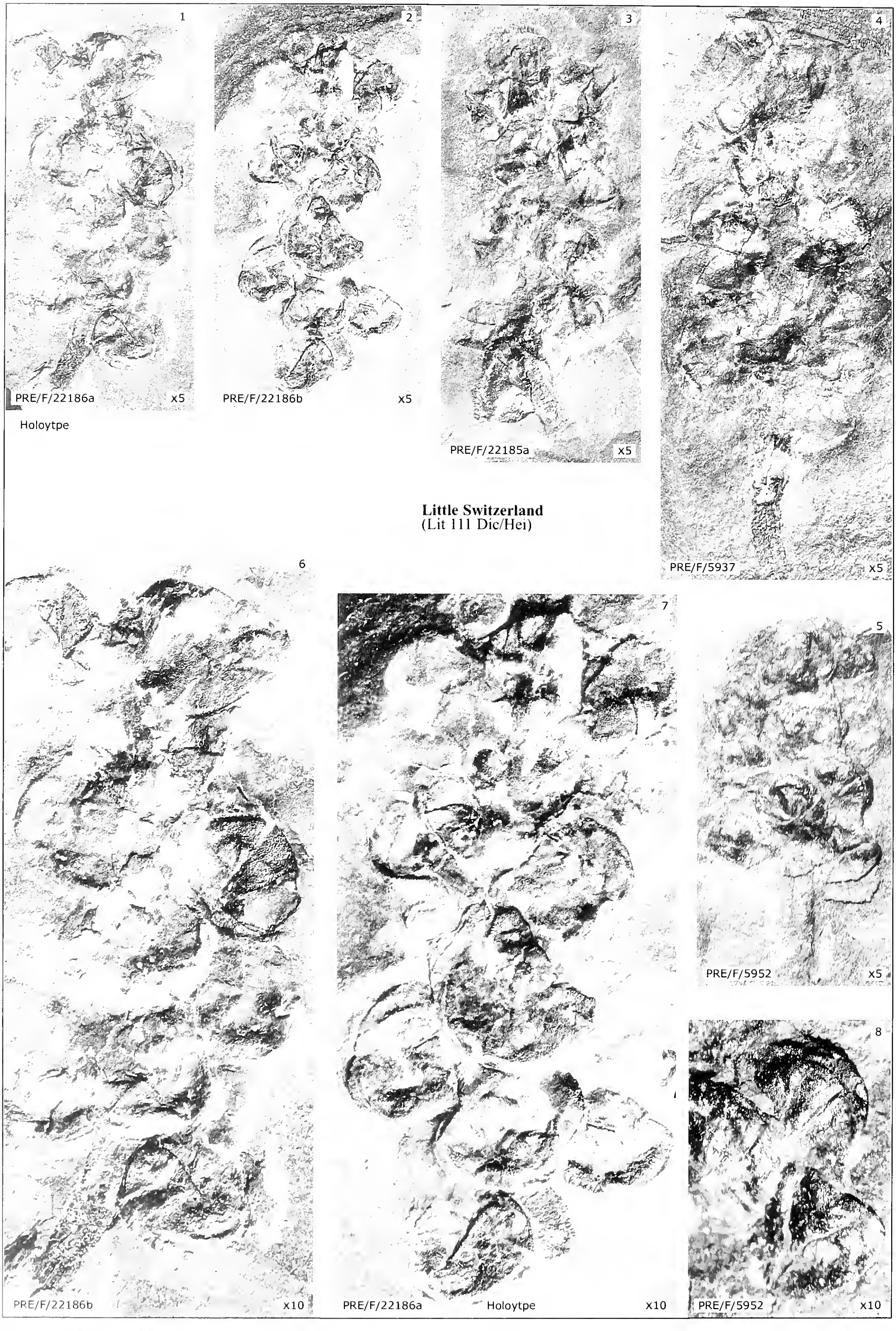


GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION

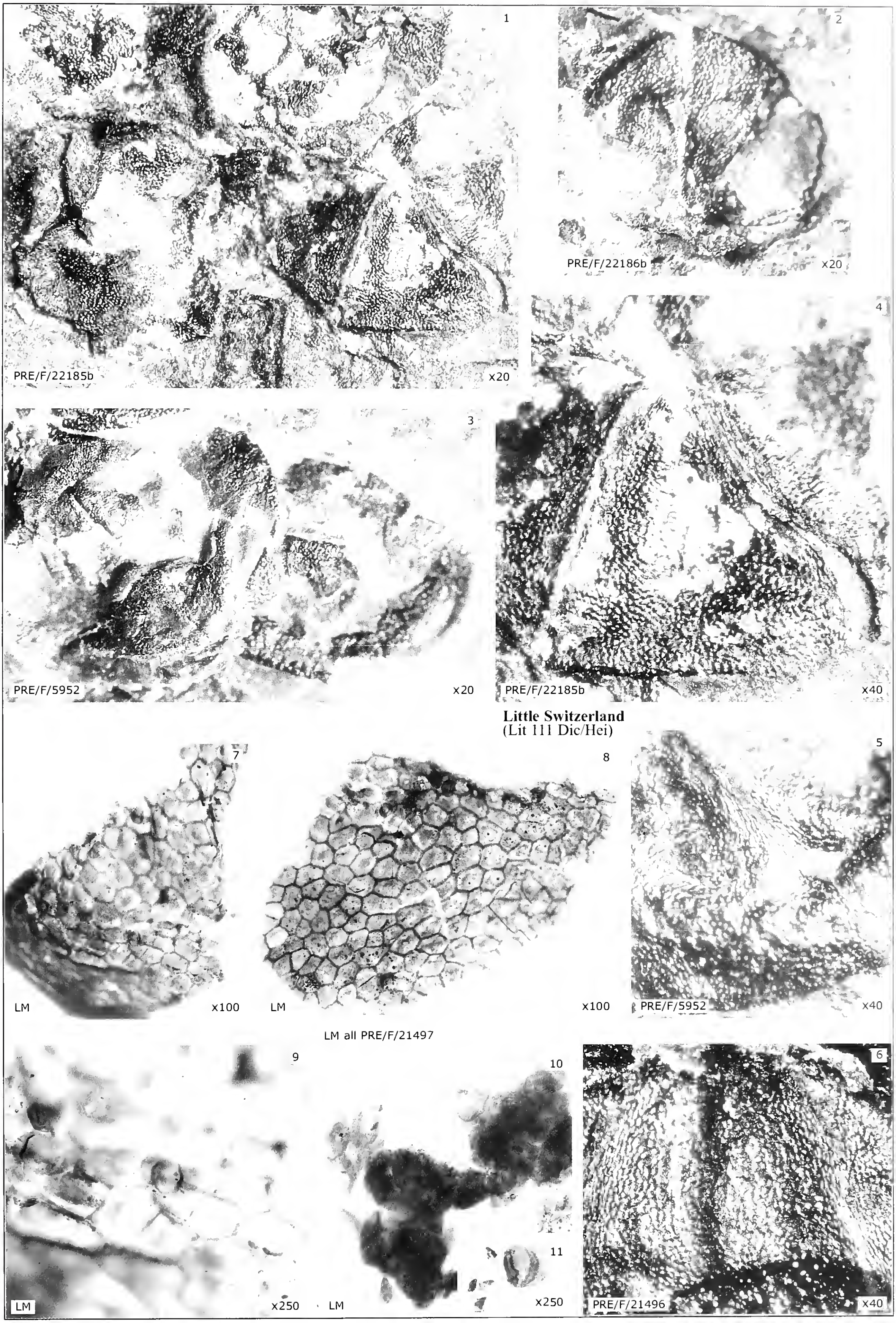








Little Switzerland
(Lit 111 Dic/Hei)



INCERTAE/PINOPSIDA **pl. 34** ***Helvetianthus tintinnabulum***

CYCADOPSIDA P.D.W.Barnard & A.G.Long 1975
CYCADALES Engl. 1892
INCERTAE SEDIS family

Androstrobus Schimp. 1870

Type species:
Androstrobus zamioides Saporta, in Schimper (1870). Etrochey, France; Bathonian, Jurassic.

Generic concept—see Saporta, in Schimper (1872, p. 199)
A cycadopsid male cone of small size, cylindrical to oval shape, and with microsporophylls bearing sessile microsporangia on abaxial surface.

Generic characters (based on the two Molteno species)
Strobilus: simple compact cone, relatively small (17–35 mm long), oval to narrowly oblong; axis stout, strongly flexed proximally, free end to 17 mm; microsporophylls helically attached, in 4 to 13 gyres of 8–10 units.
Microsporophyll: scale variously shield-shaped, apex rounded to mucronate, margins entire, face concentrically ornamented.
Microsporangium: unknown.

Etymology
Androstrobus—Andros (Gr.), male; *strobilos* (Gr.), cone.

Global range: numerous spp., Pangaea, U.Tr.–L.K.

Gondwana Triassic occurrence
SAf—Karoo Basin, 2 TCs (2 indivs).

Molteno occurrence
Frequency (F): 2 TCs (of 100 sampled in the Molteno).
Diversity (D): 2 species.
Abundance (A): 2 individuals total, very rare.

Kra 311 Dic odo: 1 indiv. in 13 man-hrs cleaving (1 per 1 man-day) very rare
Pen 321 Dic/Ris: 1 " " 35 " " (1 " 3 ") " "

The great scarcity of these cones follows the same pattern witnessed for the voltzialean male cones.

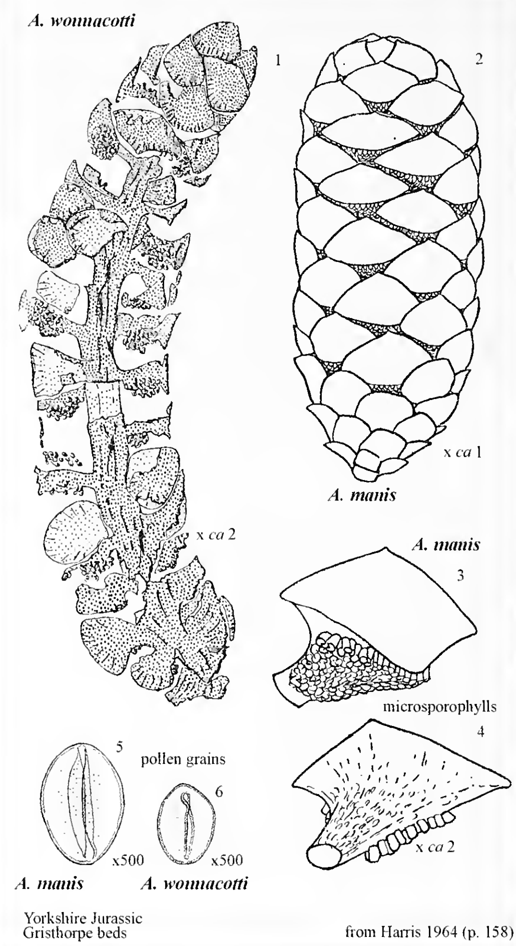
Affiliated organs (Molteno)
Female cone: unknown.
Foliage: *Pseudoctenis*—Grade 2 (Kin. reinf.).

Were the only information available that from the Molteno, it is doubtful that the affiliation between *Androstrobus* and *Pseudoctenis* would be suggested. *Pseudoctenis* (Tab. 6a), by far the most frequent and abundant of the four cycad foliage genera recognised in the Molteno, occurs in 21 TCs. In seven of these TCs it is a common (>1%) to co-dominant (>20%) element of the assemblage, yet in none does *Androstrobus* appear—an anomaly (assuming the affiliation is correct) ascribable to some undefined combination of seasonality and taphonomy (see also Tab. 45, p. 183).

Classification & comparison
Suprageneric classification (Incertae sedis/Cycadales)
Harris (1964) entertained little doubt that his *Androstrobus* specimens from the Yorkshire Jurassic represent cycads. He recognised three distinct species of these cones and affiliated them with the frond genera *Nilssonia*, *Pseudoctenis* and *Ctenis*, respectively, with varying degrees of confidence. Nor did Harris doubt that certain other species of *Androstrobus* from the Upper Triassic to Cretaceous of Europe and Russia were true cycad male cones. Hill (1990), through his work on the ultrastructure of *Androstrobus balmei*, verified the link to cycads.

Neither of the Molteno specimens is sufficiently well preserved to allow certain comparison with the Yorkshire or other *Androstrobus* material. Nor do either yield cuticle or *in situ* pollen, yet their general appearance is very like the Laurasian genus.

It is quite possible, though, that one or other of the Molteno specimens could be included in *Switzianthus* (Ginkgoopsida), or even amongst the pinopsids. The latter option seems less likely in view of the fact that we already recognise at least five genera of male conifer cones in the Molteno, but only four foliage genera.



Intactness of cones
As noted above, the two Molteno species, each based on a single cone, are known only in their intact state (tfs 1–6 opposite). The microsporangia remain unknown.

Reconstructions (Molteno species)
In the reconstructions of the two *Androstrobus* species from the Molteno, little is left to interpretation—at least as far as the general outer form of the cone is concerned. The holotype (only specimen) for each species is more or less complete—apart from the pedicel of *A. kraaiovalis*, which is conjecture.

Aside from their distal laminae, on the other hand, the morphology of the microsporophylls cannot be reconstructed and the microsporangia remain unknown.

Adaptive radiation (Molteno diversity)
The two Molteno species identified here are markedly different and distinguished according to overall shape and size of strobilus along with scale morphology. They are based on the following TCs/reference palaeodemes, which derive from the same open-woodland habitat, but from different levels within the stratigraphic sequence.

A. peninsiformis—Pen 321 Dic/Ris (Peninsula), 1 indiv.
Dicroidium open woodland; Cycle 2f (Indwe Member)
A. kraaiovalis—Kra 311 Dic odo (Kraai River), 1 indiv.
Dicroidium open woodland; Cycle 3 (Mayaputi Member)

Androstrobus peninsiformis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/13687a,b; pl. 35(1–5).
Assemblage (TC): Pen 321 Dic/Ris; Peninsula.
Preservation: virtually complete cone (apex uncertain), part and counterpart, longitudinal outer view with overlapping scales intact; 3D mould and cast in thickly laminated, medium light grey shale with poor cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimen: 1 complete indiv.

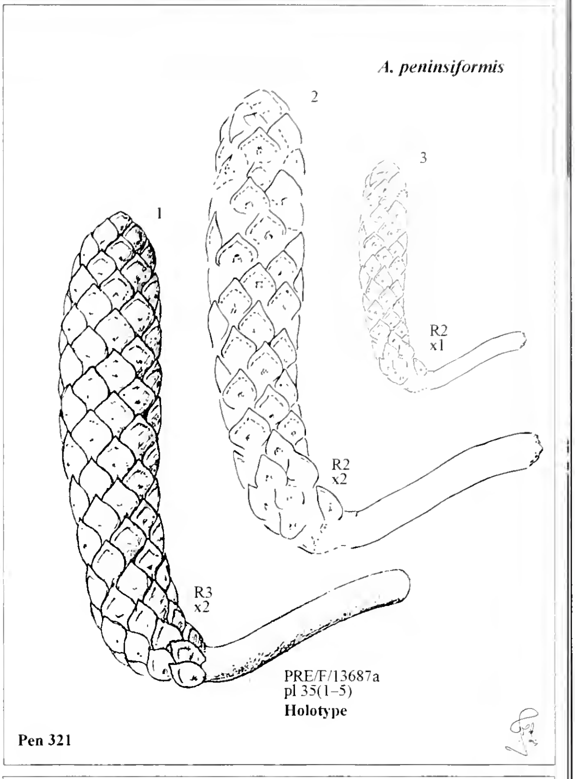
Sister palaeodemes—nil.

Specific diagnosis
An *Androstrobus* species with long cylindrical strobilus and acute-tipped, weakly ornamented microsporophylls.

Specific characters
Strobilus: narrowly oblong (38 x 8 mm).
Microsporophyll: distal lamina with mucronate apex and relatively ill-defined concentric pattern.

Etymology
peninsiformis—after the type locality, Peninsula, and the shape of the cone.

Comment & comparison—see notes for genus.



Androstrobus kraaiovalis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/8231a,b; pl. 36(1–6).
Assemblage (TC): Kra 311 Dic odo; Kraai River.
Preservation: virtually complete cone (free axis missing), part and counterpart, longitudinal outer view with overlapping scales intact; impression, clearly preserved; in grey, irregularly bedded shale.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimen: 1 intact indiv.

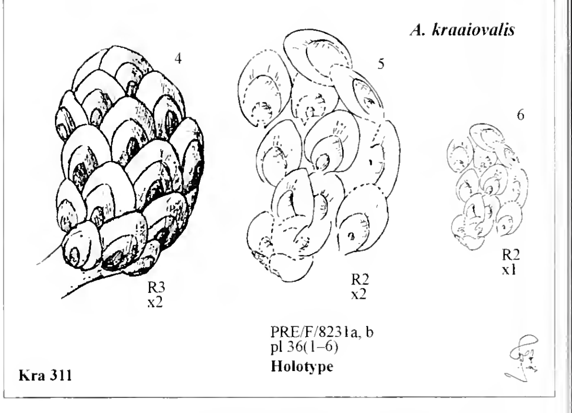
Sister palaeodemes—nil.

Specific diagnosis
An *Androstrobus* species with short oval strobilus and obtuse-tipped, strongly ornamented microsporophylls.

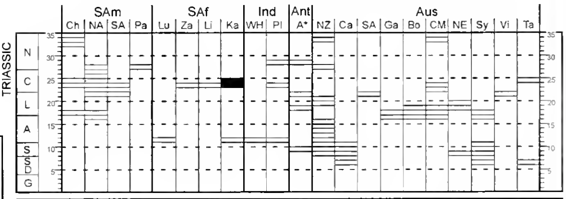
Specific characters
Strobilus: oval (20 x 11 mm).
Microsporophyll: distal lamina with rounded apex and sharply defined concentric pattern.

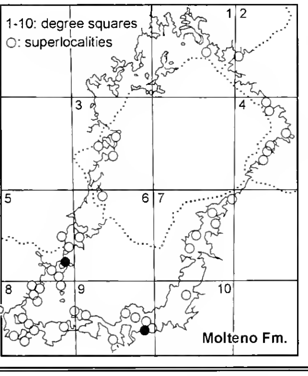
Etymology
kraaiovalis—after the type locality Kraai River, and the oval shape of the cone.

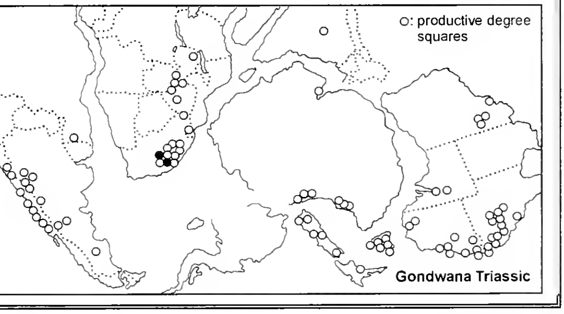
Comment & comparison—see notes for genus.

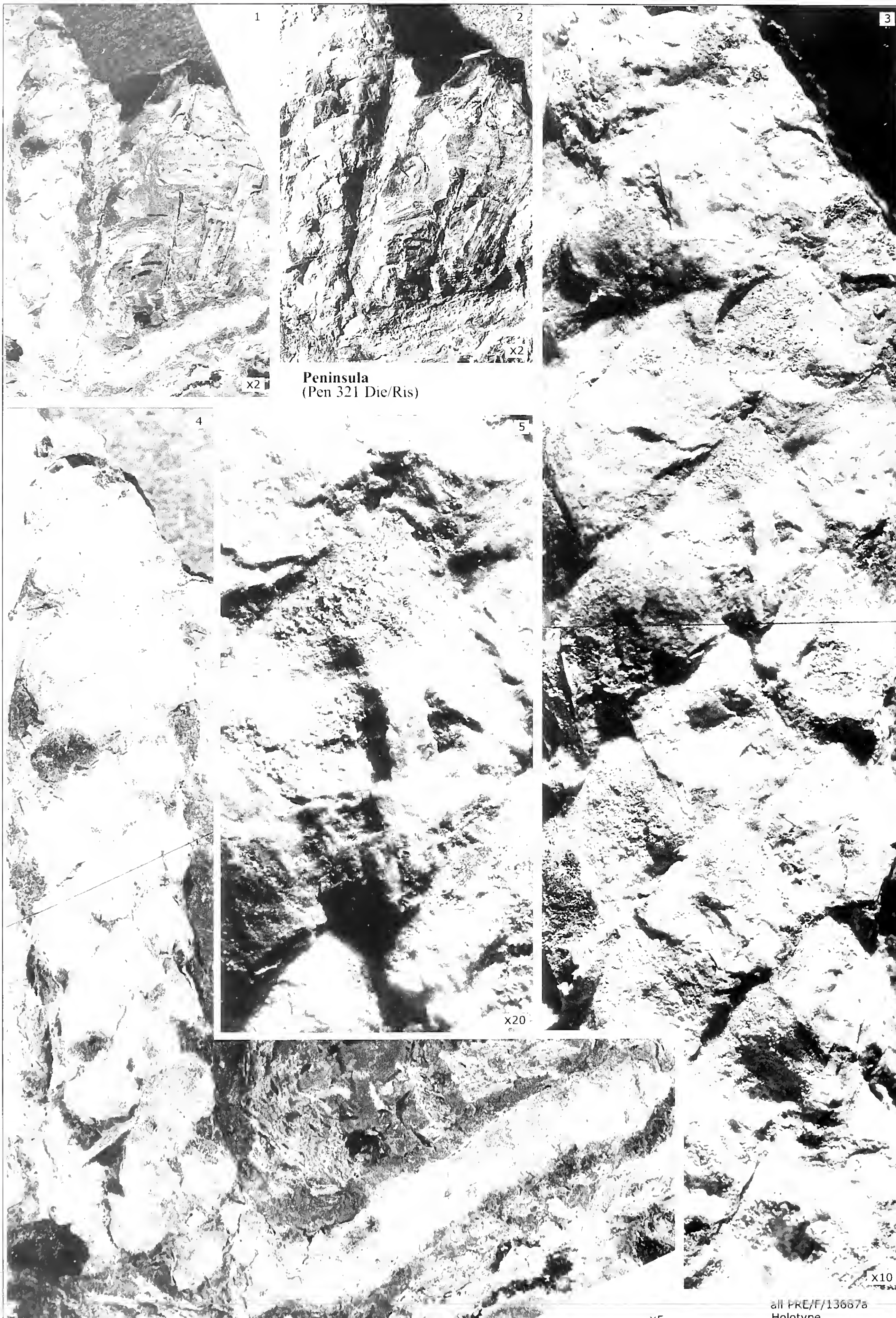


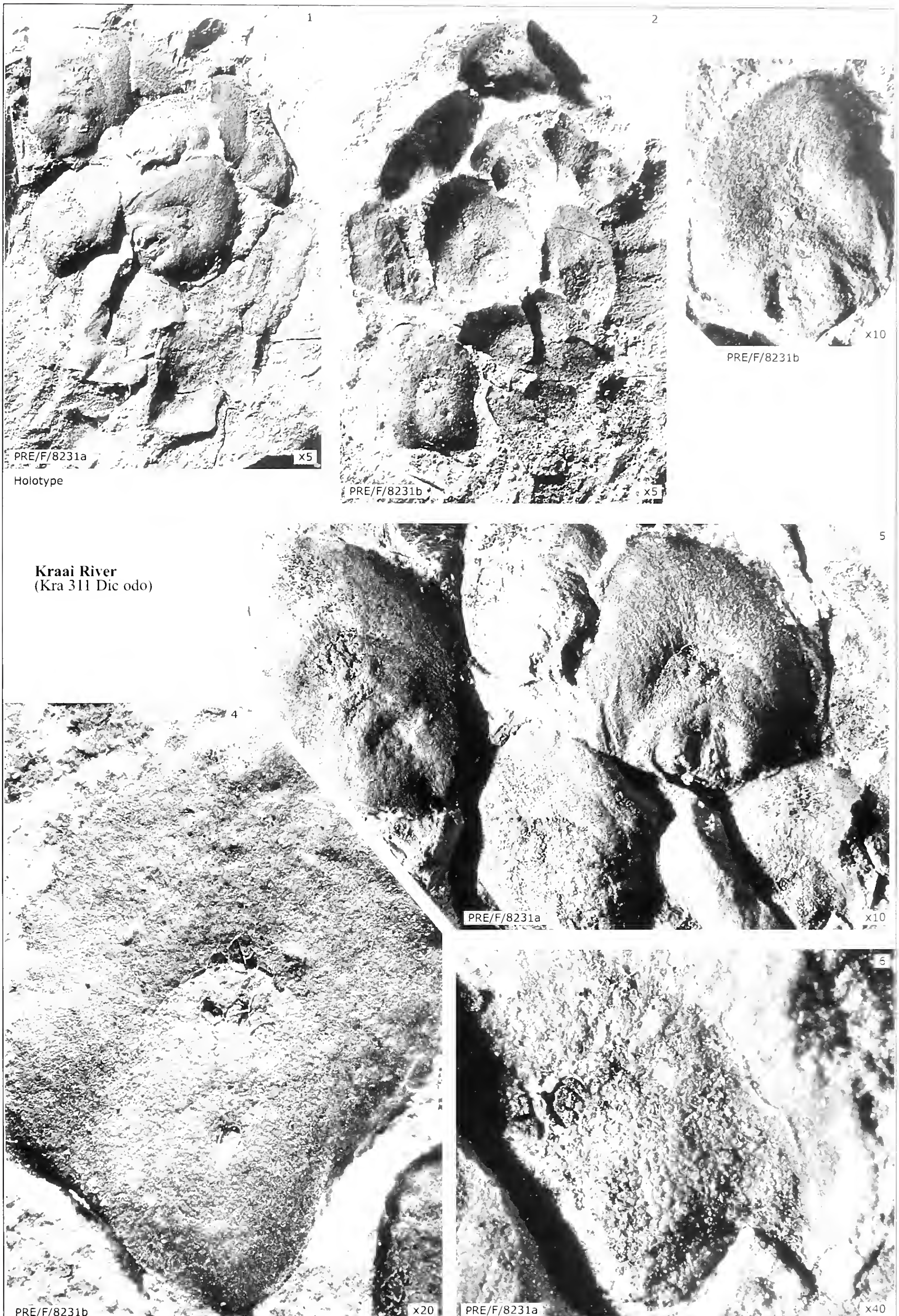
GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION








1
x2
2
x2
Peninsula
(Pen 321 Die/Ris)
3
4
5
x20
x10
x5
all PRE/F/13667a
Holotype


1
2
PRE/F/8231a
x5
Holotype
PRE/F/8231b
x5
x10
PRE/F/8231b
Kraai River
(Kra 311 Dic odo)
5
4
PRE/F/8231a
x10
6
PRE/F/8231b
x20
PRE/F/8231a
x40

CYCADOPSIDA P.D.W.Barnard & A.G.Long 1975
CYCADALES Engl. 1892
INCERTAE SEDIS family

Pseudoctenis Seward 1911

Type species
Pseudoctenis eathiensis (Richards) Seward 1911.
Upper Oolite, Scotland; Jurassic.

Generic concept (for Gondwana Triassic only)
A cycadopsid frond bearing nondehiscing pinnae with entire margins and parallel veins that fork once or twice at or near the base.

Generic characters (after Harris 1964)
Leaf: 'Leaf large, elongated, simply pinnate. Pinnae broad or narrow and elongated, lanceolate or parallel-sided, arising laterally on the rachis. Pinna margins entire, apex truncate or contracted, base expanded or contracted; veins numerous, parallel, simple or forked, not anastomosing.'
Cuticle: see And. & And. (1989, p. 281); this vol., tfs 1, 2 below.

Etymology
Pseudoctenis—pseudes (Gr.), false; *ctenis*, a fossil cycad genus.

Global range: numerous spp., Pangaea, U. Tr.–U. K.

Gondwana Triassic occurrence
Diversity (D): 11 foliage species.
Ubiquity (U): 3 continents (of 5 comprising Gondwana).
Frequency (F): 16 degree squares (of the 84 across Gondwana).
Abundance (A): 3% (the norm in Molteno TCs).
Longevity (L): 14 myrs (Lower Anisian to Lower Carnian).

Colonisation success: FUDAL rating 16/3/11/3/14 = 47.
Intermediate success (Grade 3); *Pseudoctenis* was the ninth most prominent genus in the Gondwana Triassic; it was diverse, but of only moderate ubiquity, frequency, abundance and longevity.
Endemism: of the 11 Gondwana Triassic species, six occur more or less widely through the realm, 1 is a basin endemic, and four are single-assemblage endemics.

Molteno occurrence
Frequency (F): 21 TCs (of 100 sampled in the Molteno).
Diversity (D): 9 species.
Abundance (A): co-dominant (21–25%) in 2 TCs; occasional to common (1–3%) in 2 TCs; and <1% in the other 17 TCs.

Habit: probably a cycad-like plant.
Preferred habitat: The genus occurs mostly in high diversity assemblages that are generally *Dicroidium*-dominated and probably represent forest and woodland associations of the riverbank (levee) and other relatively elevated ground.

Affiliated organs
Female strobilus: unknown
Male strobilus: *Androstrobus*—Grade 2 (Kin. reinf.); see note under *Androstrobus* (p. 136).

Classification & comparison (adapted from And. & And. 1989, p. 280)
Intergeneric comparisons
Gondwana Triassic cycadalean genera—The four genera (*Pseudoctenis*, *Jeanjacquesia*, *Ctenis* and *Moltenia*) of Molteno cycads are clearly distinguished both on the basis of mega- and micromorphological characters. The cuticle, in particular, provides an indication of the taxonomic distance between the genera. They are considered here as probably representing four distinct families (p. 54). The reproductive organs remain unknown, thus shedding no light on the matter.

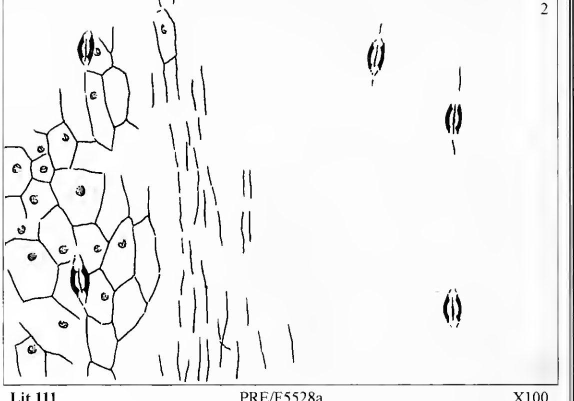
Other cycadalean genera—We have elected not to employ the genus *Nilssonia* which has been shown by Meyen (1984) to be a form-genus affiliating with distinctly different types of female reproductive structures. In our Gondwana Triassic hypodigms (And. & And. 1989) entire fronds that might have been included as *Nilssonia* are listed under *Taeniopteris* and segmented fronds under *Pseudoctenis*.

Bennettitalean (cycadeoid) genera—*Pseudoctenis* is distinguished from the bennettitalean genus *Pterophyllum* solely on the basis of its cuticle. It must be noted, though, that for the great majority of the Molteno and Gondwana Triassic fronds identified as *Pseudoctenis* there exists no preserved cuticle.

Interspecific comparisons
We assumed in And. & And. (1989) that the greater proportion of the 11 Gondwana Triassic *Pseudoctenis* species recognised were closely related within the scope of a natural genus. In view, however, of the paucity of cuticle (poor material from only two of the nine Molteno species has been obtained) and lack of affiliated fruit, there remains no way of confirming this view.

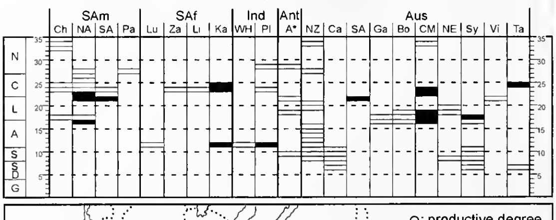
The nine *Pseudoctenis* species from the Molteno are quite distinctive when only their reference palaeodemes are considered, but the position becomes far less clear when all 25 palaeodemes from 15 assemblages are taken into account. The morphological ranges seen in the different palaeodemes overlap in a complex fashion: rarely do those of any two palaeodemes approximately coincide.

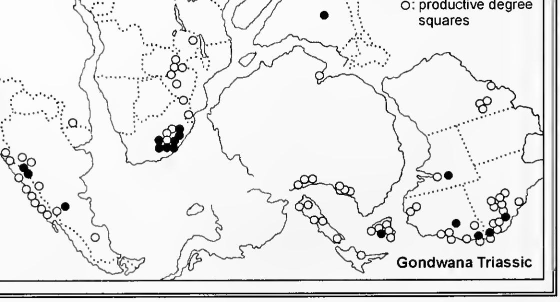
P. harringtoniana



Lit 111 PRE/F5528a X100

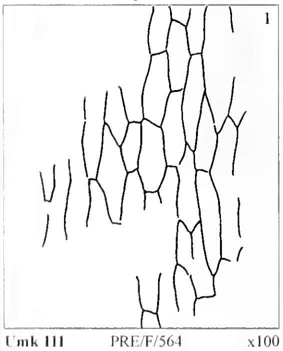
GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION



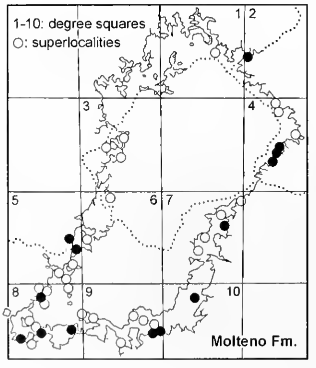


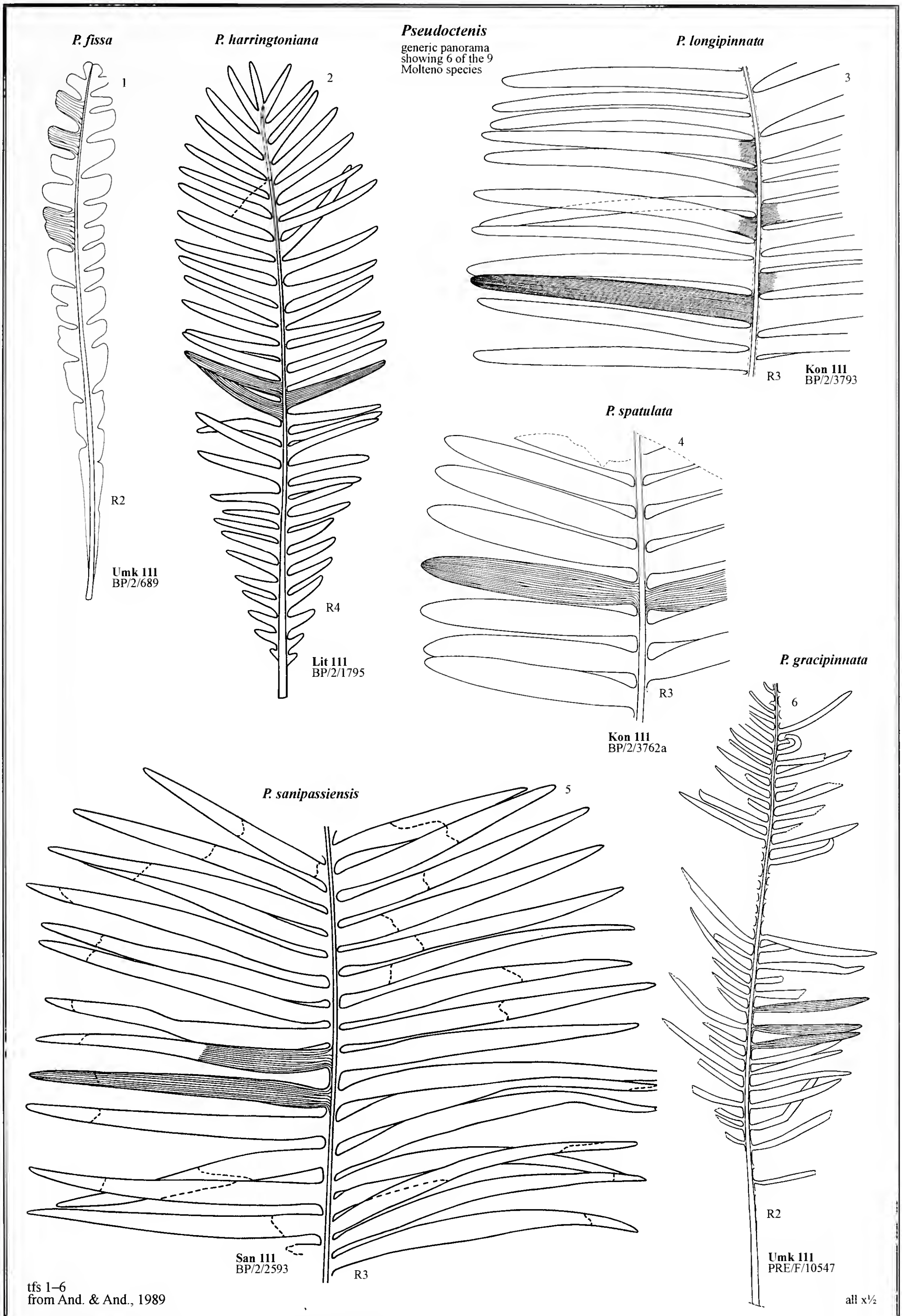
tfs 1 & 2 from And. & And., 1989

P. fissa



Umk 111 PRE/F/564 x100




Pseudoctenis
generic panorama
showing 6 of the 9
Molteno species
P. fissa
1
R2
Umk 111
BP/2/689
P. harringtoniana
2
R4
Lit 111
BP/2/1795
P. longipinnata
3
R3
Kon 111
BP/2/3793
P. spatulata
4
R3
Kon 111
BP/2/3762a
P. sanipassiensis
5
San 111
BP/2/2593
R3
P. gracipinnata
6
R2
Umk 111
PRE/F/10547
tfs 1–6
from And. & And., 1989
all x½

CYCADOPSIDA P.D.W.Barnard & A.G.Long 1975
CYCADALES Engl. 1892
INCERTAE SEDIS family

Jeanjacquesia J.M.And. & H.M.And. 1989

Type species
Jeanjacquesia switzipinnata J.M.And. & H.M.And. 1989.
Little Switzerland, Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis
A cycadopsid frond bearing readily dehiscing pinnae with entire margins and parallel veins that fork only once at or near the base.

Generic characters [based on *J. switzipinnata & J. spA* (Bir 111)].
Leaf: relatively large, shape unknown, simply pinnate; pinnae readily detach (attachment unknown), margins entire, linear oblong, apex unknown, base contracted, asymmetrical; veins moderately to relatively well spaced, parallel and not meeting lamina margin, simple or forked near base, not anastomosing.
Cuticle: see And. & And. (1989, p. 337); this vol., tfs. 3–6 opposite.

Eponymy
Jeanjacquesia—after Jean-Jacques Rousseau, French philosopher.

Global range: 3 spp., Gondwana, Tr. (ANI–NOR).
First & Last: the three Molteno species.

Gondwana Triassic occurrence
Frequency (F): 3 degree squares (of the 84 across Gondwana).
Ubiquity (U): 1 continent (of 5 comprising Gondwana).
Diversity (D): 3 foliage species.
Abundance (A): <1% (the norm in Molteno TCs).
Longevity (L): 2 myrs (Carnian).
Colonisation success: FUDAL rating 3/1/3/–/2 = 9.
Minimum success (Grade 1): *Jeanjacquesia* was the 23rd most prominent genus in the Gondwana Triassic; it was of very low frequency, ubiquity, diversity, abundance and longevity.
Endemism: all three species are single-assemblage endemics.

Molteno occurrence
Frequency (F): 3 TCs (of 100 sampled in the Molteno).
Diversity (D): 3 species.
Abundance (A): extremely to vanishingly rare (<1%) in the 3 TCs.
Habit: probably a cycad-like plant.
Preferred habitat: the type species, *J. switzipinnata*, is a very rare element (six individuals collected) in the Lit 111 Dic/Hei assemblage, which is dominated in particular by *Dicroidium odontopteroides*. It most likely occupied the understorey of the riverine forest.

Affiliated organs—unknown.

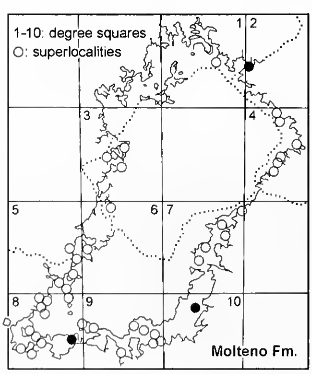
Classification & comparison (adapted from And. & And. 1989, p. 336)
Intergeneric comparisons
Gondwana Triassic cycadalean genera—*Jeanjacquesia*, on the basis of both general morphology and cuticle, is quite distinct from the other four Gondwana Triassic cycad genera. It is most like *Pseudoctenis*, but the latter differs in having pinnae with symmetrical bases that do not dehisce.

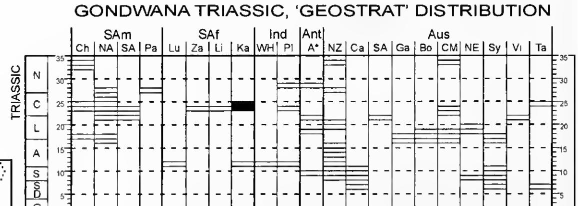
Other cycadalean genera—*Jeanjacquesia* does not exhibit the heavily developed pinna base usually seen in the extant cycad genera (e.g. *Encephalartos*, *Zamia*) that occasionally drop their pinnae. *J. switzipinnata* does have typically cycadaceous cuticle, which, in its perfectly hypostomatic nature, its well developed guard cells, cutinised subsidiary cells and strongly curved cell walls, particularly resembles *Zamia* (Greguss 1968). Its cuticle shows less similarity to any of the Yorkshire Jurassic cycad genera.

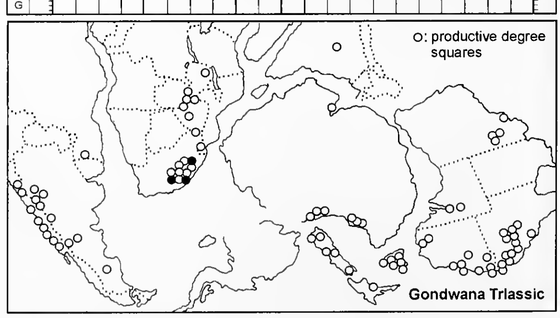
Bennettitalean (cycadeoid) genera—*Zamites* and *Otozamites* are the cycadeoid genera most similar to *Jeanjacquesia*, but *Zamites* has an essentially symmetrical base, while that of *Otozamites* is strongly asymmetrical, with the upper angle developed into an auricle. Both have somewhat spreading venation and both have typically cycadeoid cuticle.

Interspecific comparisons
The two species, *J. switzipinnata* and *J. spA*, are sufficiently similar to appear to belong to a single natural genus, but since cuticle is known only for the former and fruit for neither, this cannot be confirmed.
J. spB, based on a single Molteno (Maclear) specimen in Du Toit's collections (Du Toit 1927), was placed in *Jeanjacquesia* for convenience in And. & And. (1989), but might equally tentatively have been included in *Zamites* (cycadeoid), *Pseudoctenis* (cycad), or some unnamed genus. It is not illustrated in the present volume.
Each species is represented solely by the reference palaeodeme.

GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION







The Cycadales at family level

The extant cycads are included in three families (Stevenson 1990, 1992):

Cycadaceae—1 genus (*Cycas*), 14 species.
Stangeriaceae—1 genus (*Stangeria*), 2 species.
Zamiaceae—8 genera (*Encephalartos*, *Zamia* etc.), *ca* 110 species.

In an attempt to resolve, however imperfectly, the possible family-level taxonomy of the four Molteno cycad foliage genera, we are limited to a consideration of their general morphology and cuticular features. Female cones from the formation (and, indeed, the entire Gondwana Triassic) remain unknown, while supposed male cones are represented by only two individuals that are very uncertainly affiliated with the foliage genus *Pseudoctenis*.

Though exceptions must be acknowledged, and though diagnosed on the basis of their female cones, the three extant families can be separated reasonably successfully on consideration of their foliage morphology and cuticles alone (Greguss 1968). The Cycadaceae (*Cycas*) species all have linear leaves with a single distinct vein or midrib and cuticles showing large pits along the cell walls; the Stangeriaceae (*Stangeria*) species have taeniopteroid leaves and cuticles with meandering cell walls; while the Zamiaceae sport parallel-veined leaves and cuticles with gently curved to sinuous cell walls.

In the light of the above, it seems that the most likely option is to consider each of the four Molteno genera to represent a different cycad family within a vigorously sprouting cycadopsid phylogenetic tree following the end-Permian extinction. A comparative study of their foliage morphology and cuticles, outlined below, suggests that they are as distinct from one another as are the core genera characterising the extant families:

Pseudoctenis (9 Molteno species)
Leaves—pinnae not dehiscing, entire, with parallel venation.
Cuticle—cell walls relatively straight, subsidiary cells apparently undifferentiated.

Moltenia (4 Molteno species)
Leaves—pinnae not dehiscing, toothed, with parallel venation.
Cuticle—cell walls, strongly undulating, subsidiary cells apparently undifferentiated.

Jeanjacquesia (3 Molteno species)
Leaves—pinnae dehiscing, entire, with parallel venation.
Cuticle—cell walls distinctly sinuous, subsidiary cells highly developed and well-cutinised.

Ctenis (2 Molteno species)
Leaves—pinnae dehiscing or not dehiscing, margins lobed or irregular, with clearly anastomosing venation.
Cuticle—cell walls strongly sinuous to meandering (stomata unknown).

Alternative suprageneric taxonomic options quite obviously exist, but short of well-affiliated fruiting material no certain conclusions are possible. HMA, for instance, feels that the available evidence is insufficient to differentiate families.

Jeanjacquesia

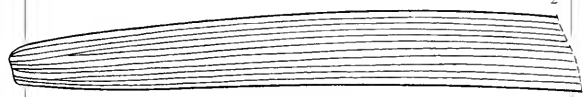
generic panorama showing
2 of the 3 Molteno species

1

BP/2/4883 — *Jeanjacquesia* spA — R2 x1

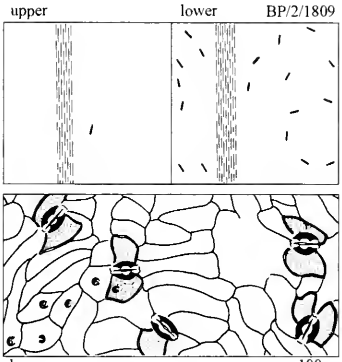
Bir 111

2

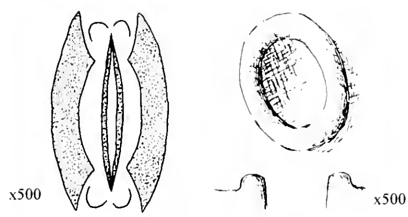


BP/2/1809 — *J. switzipinnata* — R2 x1

3



4

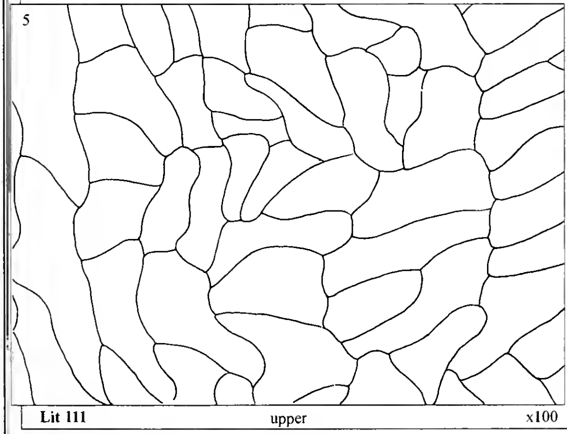


Lit 111

tfs 1–6 from And. & And., 1989

BP/2/2030

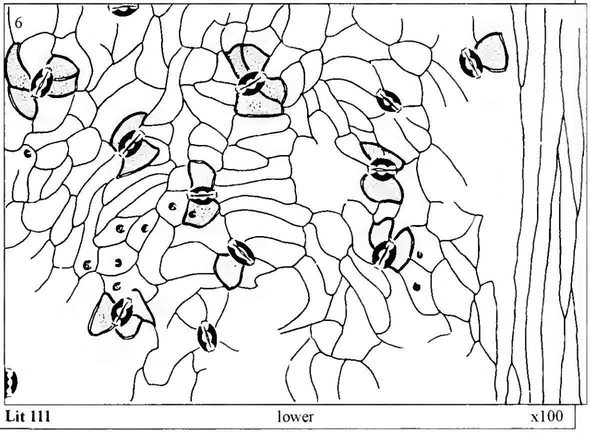
5



Lit 111 upper x100

BP/2/1809

6



Lit 111 lower x100

CYCADOPSIDA P.D.W.Barnard & A.G.Long 1975
CYCADALES Engl. 1892
INCERTAE SEDIS family

Ctenis Lindl. & Hutton 1834

Type species
Ctenis falcata Lindl. & Hutton 1834.
Yorkshire, England; Jurassic.

Generic concept (for Gondwana Triassic only)
A cycadopsid frond bearing essentially nondehiscing pinnae with entire to irregular margins and parallel veins that fork and clearly anastomose throughout the lamina length.

Generic characters (adapted from Harris 1964)
Leaf: shape and size not given, once pinnate; pinnae usually with entire margins, inserted laterally on the rachis, shape (including apex and base) and base not given; veins several, more or less parallel, anastomosing, meeting lamina margin.
Cuticle: see And. & And. (1989, p. 342); this vol., tfs 3, 4 opposite.

Etymology
Ctenis—Ktenos (Gr.), comb.

Global range: numerous spp., Pangaea, Tr.–K.

Gondwana Triassic occurrence
Frequency (F): 4 degree squares (of the 84 across Gondwana).
Ubiquity (U): 3 continents (of 5 comprising Gondwana).
Diversity (D): 2 foliage species.
Abundance (A): <1% (the norm in Molteno TCs).
Longevity (L): 2 myrs (Lower Carnian).

Colonisation success: FUDAL rating 4/3/2/–/2 = 11.
Minimum success (Grade 1): *Ctenis* was the 22nd most prominent genus in the Gondwana Triassic; it was fairly ubiquitous and of very low frequency, diversity, abundance and longevity.
Endemism: the two Molteno species are single-assemblage endemics (the non-Molteno specimens are not identifiable to species).

Molteno occurrence
Frequency (F): 2 TCs (of 100 sampled in the Molteno).
Diversity (D): 2 species.
Abundance (A): very rare to vanishingly rare (<1%) in the 2 TCs.

Habit: probably a cycad-like plant.
Preferred habitat: The two *Ctenis* species from the Molteno Fm. occur in high diversity assemblages: the one being very rare from Kon 211/221 dominated by *Asterotheca* and *Pseudoctenis*, the other vanishingly rare from Umk 111 dominated by *Dicroidium odontopteroides*.

Affiliated organs—unknown.

Classification & comparison (adapted from And. & And. 1989, p. 342)
Intergeneric comparisons

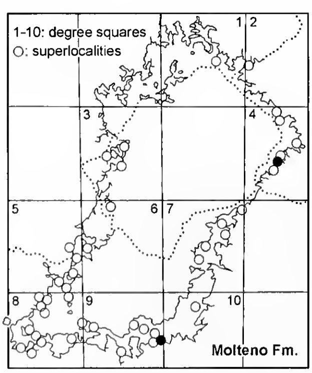
Gondwana Triassic cycadalean genera—Ctenis, on frond morphology, is readily distinguished from the other four Gondwana Triassic cycad genera. There is no particular genus that it resembles most closely.

Other cycadalean genera—We are unaware of any other cycad genera, extinct or extant, in which anastomosing venation is a diagnostic characteristic. It should be noted, though, that the extant genus *Stangeria* (with a single species) and at least two of the 30 species of the extant *Encephalartos* show venation with occasional anastomoses.

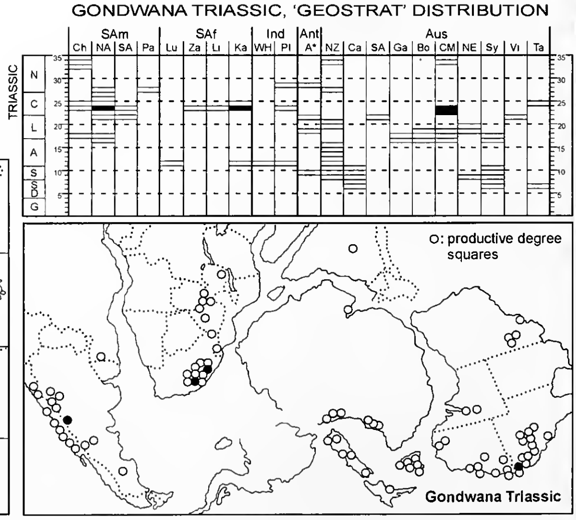
Bennettitalean (cycadeoid) genera—Dictyozamites is the only cycadeoid genus with anastomosing venation, but it is otherwise quite unlike *Ctenis* in that the pinnae are strongly contracted at the base (which is asymmetrical) leaving only a narrow section attaching to the rhachis.

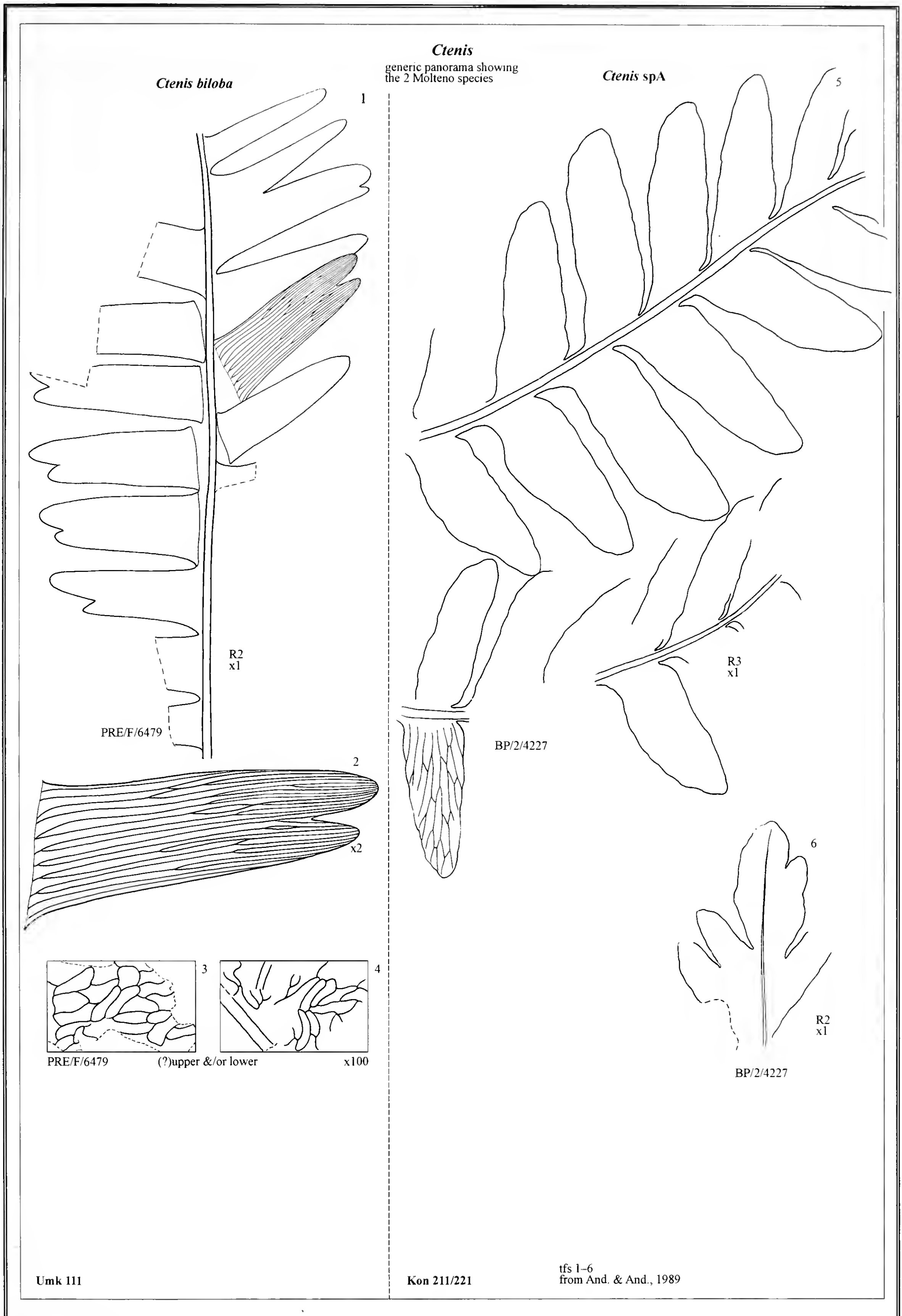
Interspecific comparisons
The two species from the Molteno identified as belonging to the pandemic genus *Ctenis* may be quite unrelated. *C. biloba* has produced tiny fragments of cuticle which do not exclude identity with *Ctenis*. Neither species has affiliated fruit.

The reference palaeodemes of the two species, consisting of only one and two individuals respectively, are distinctly dissimilar. No additional palaeodemes occur.



GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION





Ctenis
generic panorama showing the 2 Molteno species
Ctenis biloba
Ctenis spA
1
R2
x1
PRE/F/6479
2
x2
3
4
PRE/F/6479
(?)upper &/or lower
x100
5
R3
x1
BP/2/4227
6
R2
x1
BP/2/4227
Umk 111
Kon 211/221
tfs 1–6
from And. & And., 1989

CYCADOPSIDA P.D.W.Barnard & A.G.Long 1975
CYCADALES Engl. 1892
INCERTAE SEDIS family

Moltenia A.L.du Toit

Type species
Moltenia dentata A.L.du Toit 1927.
Umkomaas Valley, Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis
A cycadopsid frond bearing nondehiscing pinnae with toothed margins and parallel veins that fork in the proximal half to two-thirds of the lamina.

Generic characters (based on the four Gondw. Trias. species)
Leaf: small to large, shape uncertain (apparently narrowly ovate in one species), once pinnate; pinnae laterally attached, margins variously toothed, narrowly elliptic, apex usually irregularly toothed, base markedly contracted; veins closely (1 spp.) to well spaced (3 spp.), spreading to meet lamina margin at each tooth, repeatedly forking but not anastomosing.
Cuticle: see And. & And. (1989, p.348); this vol., tf. 2 opposite.

Etymology
Moltenia—named by Du Toit in reference to the Molteno Fm.

Global range: 4 spp., Gondwana, M.–U.Tr. (LAD–CRN).
First: *Moltenia* (*Pseudoctenis wardii*) (Artabe 1985); Los Menucos Fm., southern Argentina, South America.
Last: the three Molteno species (And. & And. 1989).

Gondwana Triassic occurrence
Frequency (F): 4 degree squares (of the 84 across Gondwana).
Ubiquity (U): 3 continents (of 5 comprising Gondwana).
Diversity (D): 4 foliage species.
Abundance (A): <1% (the norm in Molteno TCs).
Longevity (L): 4 myrs (Upper Ladinian to Lower Carnian).
Colonisation success: FUDAL rating 4/3/4/–/4 = 15.
Limited success (Grade 2): *Moltenia* was the 20th most prominent genus in the Gondwana Triassic; it was fairly ubiquitous but of very low frequency, diversity, abundance and longevity.
Endemism: of the four Gondwana Triassic species, one is known from two continents, one is a single-basin endemic, and two are single-assemblage endemics.

Molteno occurrence
Frequency (F): 5 TCs (of 100 sampled in the Molteno).
Diversity (D): 4 species.
Abundance (A): very rare to vanishingly rare (<1%) in all 5 TCs.
Habit: probably a cycad-like plant.
Preferred habitat: The genus occurs as a particularly rare component in high to very high diversity assemblages. Those assemblages from Hlatimbe, Umkomaas and Little Switzerland, in which it occurs, are all dominated by *Dicroidium* and in three of five cases by *D. odontopteroides*. All four species of *Moltenia* most likely occupied the understorey of riverine forest.

Affiliated organs—unknown.

Classification & comparison (adapted from And. & And. 1989, p. 346)
Intergeneric comparisons
Gondwana Triassic cycadalean genera—Moltenia, on both general frond morphology and cuticle, is readily distinguished from the other four Gondwana Triassic cycad genera. It is most like *Pseudoctenis*, but the latter differs in the pinnae having entire margins and parallel venation, and in the epidermal cell walls being straight rather than strongly sinuous.

Other cycadalean genera—In the toothed nature of the pinna margin, *Moltenia* is very like the extant South African cycad genus *Encephalartos*, but in the attachment of the pinnae it is markedly different. The epidermal cell walls of *Encephalartos* are gently curved, not strongly sinuous as in *Moltenia*.

Bennettitalean (cycadeoid) genera—Moltenia, in general frond morphology, does not resemble any of the cycadeoids. While it does display sinuous cell outlines, these do not approach the typical close meandering as witnessed in the cycadeoids; nor do any other typical cuticular features of the latter order appear.

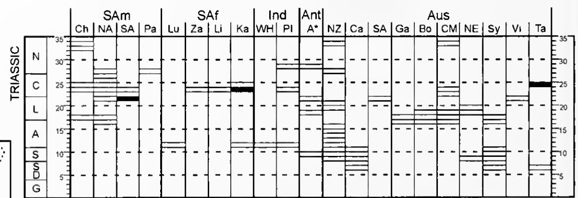
Interspecific comparisons
The four species comprising *Moltenia* give the clear impression of representing a single natural genus, but this cannot be confirmed either on the basis of cuticle (known for only one species) or affiliated cones (unknown).

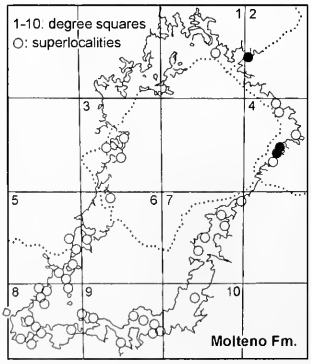
The reference palaeodemes (RPs) of the four species are markedly distinct. The three additional palaeodemes (sister palaeodemes, SPs), representing two of the species, are readily compared to the relevant RPs, hence supporting rather than confusing the recognition of species.

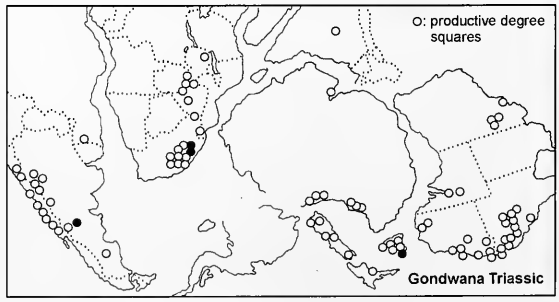
Species	Ref. Pal.	indivs (in RPs)	indivs (in SPs)
M. dentata	Umk 111	18	1 (Lit 111)
M. paucidentata	"	1	–
M. feistmantelii	Hla 213	5	–
M. gracilidentata	"	1	6 (Hla 211, Hla 212)

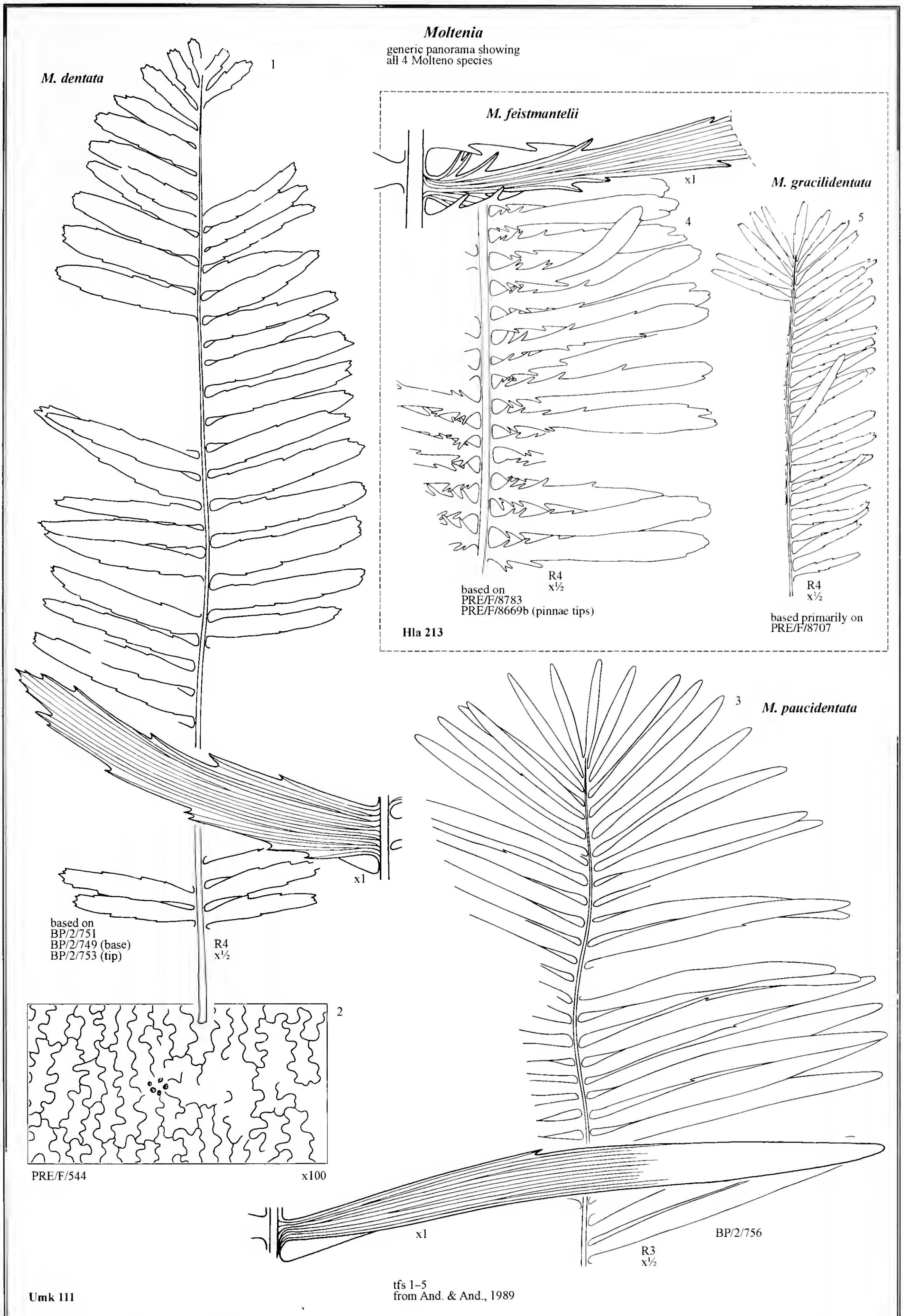
***Moltenia* species & abundance, Molteno Fm.**

GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION








Moltenia
generic panorama showing
all 4 Molteno species
M. dentata
1
based on
BP/2/751
BP/2/749 (base)
BP/2/753 (tip)
R4
x½
x1
2
PRE/F/544
x100
M. feistmantelii
x1
4
R4
x½
based on
PRE/F/8783
PRE/F/8669b (pinnae tips)
Hla 213
M. gracilidentata
5
R4
x½
based primarily on
PRE/F/8707
3
M. paucidentata
x1
BP/2/756
R3
x½
tfs 1–5
from And. & And., 1989
Umk 111

GINKGOOPSIDA S.V.Meyen 1987
PELTASPERMALES F.Nèmejc 1968
PELTASPERMACEAE H.H.Thomas ex T.M.Harris 1937

Peltaspermum T.M.Harris 1937

Synonym: *Meyenopteris* R.J.Poort & J.H.F.Kerp 1990.

Type species
Peltaspermum rotula T.M.Harris 1937.
Tancredia River (*Lepidopteris* Bed), Scoresby Sound, E. Greenland; Rhaetic, U. Triassic.

Generic concept
A ginkgoopsid strobilus of linear-cylindrical shape with megasporophylls of one to five peltate multilobed discs bearing abaxial ovules.

Generic characters (Molteno Fm.)
Strobilus: simple, racemose, compact, radially symmetrical, of medium size (*ca* 100–175 mm long); axis relatively gracile, generally slightly curved; megasporophylls numerous, helically arranged.
Megasporophyll: simple to compound, pedunculate; ovuliferous discs peltate (4–8 mm diam.), radially symmetrical, with or without distinct apical cap, multilobed (6–12 lobes); ovules/seeds abaxial, naked, pendent, 1 per lobe.
Ovule/seed: tetrahedral (2 x 1 mm), unwinged, with bifid micropyle.

Etymology
Peltaspermum—*pelta* (Lat.), small shield; *sperma* (Gr.), seed, with reference to the peltate ovuliferous discs.

Global range: numerous spp., Pangaea, U.P.–L.K.

Gondwana Triassic occurrence
SAm—N. Argentina, 2 TCs (2 indivs).
SAf—Karoo Basin, 17 TCs (>200 indivs).
Aus—New South Wales & Victoria, 3 TCs (3 indivs).

Molteno occurrence
Frequency (F): 17 TCs (of 100 sampled in the Molteno).
Diversity (D): 4 species.
Abundance (A): 257 individuals total, rare to extremely rare in top 8 TCs.

Kon 222 Dic odo:	24	indivs	in	40	man-hrs	(6	per	1	man-day)	rare
Aas 411 Dic/Sph:	88	"	"	512	man-hrs	(1–2	per	1	man-day)	very rare
Bir 111 Sph 2spp:	67	"	"	550	"	(1–2	"	1	")	"
Tel 111 Hei elo:	14	"	"	90	"	(1–2	"	1	")	"
Maz 211 Hei/Dic:	9	"	"	85	"	(1	"	1	")	"
Mat 111 Dic dub:	4	"	"	65	"	(1	"	1	")	"
Umk 111 Dic 2spp:	17	"	"	400	"	(1	"	3	")	"
Lit 111 Dic/Hei:	11	"	"	550	"	(1	"	5	")	extr. rare

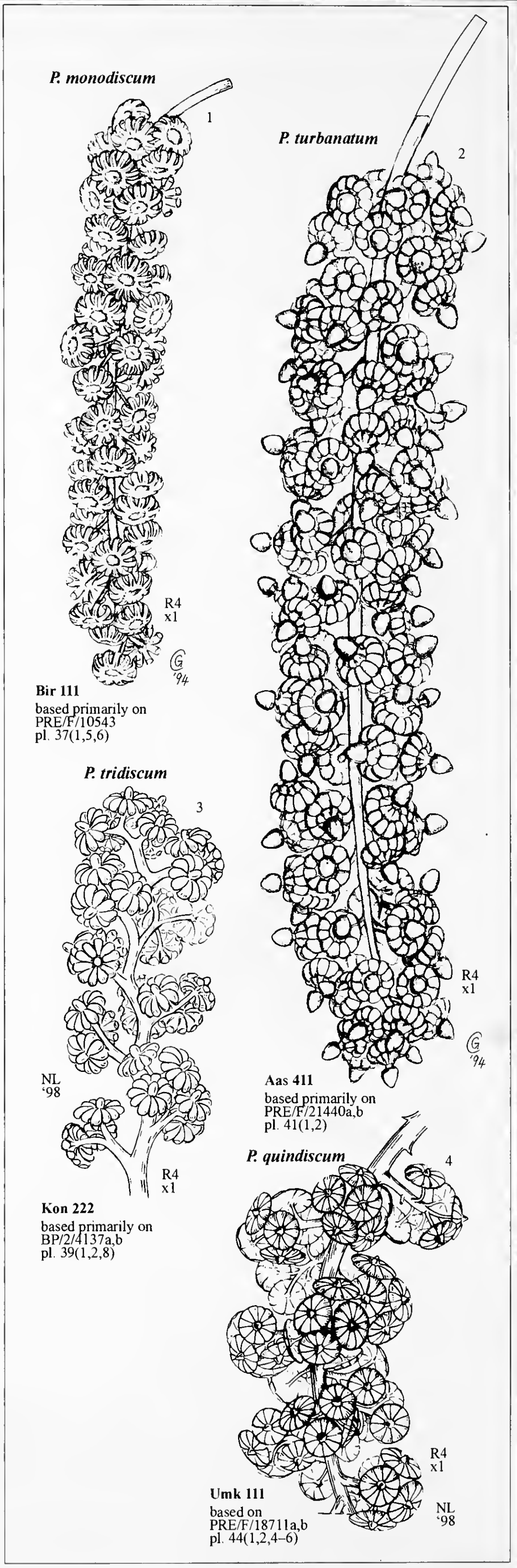
Peltaspermum is very much more common in the two lake deposits (Aas 411 and Bir 111) than in the *Dicroidium* riparian forest habitats (Umk 111 and Lit 111).

Affiliated organs
Male strobilus: *Antevsia*—Grade 3 (Kin. reinf., Mut. occ.).
Foliage: *Lepidopteris*—Grade 4 (Mor. corr., Cut. corr.).

Classification & comparison
Suprageneric classification (Peltaspermaceae/Peltaspermales)
The prominent early Mesozoic pteridosperms, including *Peltaspermum*, *Umkomasia* (corystosperm) and *Caytonia*, have been very variously classified. Crane (1985, 1988), on the basis of cladistic analysis, found the corystosperms more closely related to the glossopterids and *Caytonia* than to the peltasperms. Meyen (1987) included the families Umkomasiaceae (= Corystospermaceae) and Peltaspermaceae within the order Peltaspermales, and identified the Caytoniales as a separate order. Stewart & Rothwell (1993) included the families Corystospermaceae and Peltaspermaceae in the order Caytoniales. Taylor & Taylor (1993) treated the Corystospermales, Peltaspermales and Caytoniales as separate orders. In And. & And. (1989, pp. 64–67), we followed Meyen's classification, finding the cuticle of the corystosperm and peltasperm foliage compellingly similar.

In the light of our present study, we consider the *Umkomasia* and *Peltaspermum* strobili clearly distinct at order level—in line with Taylor & Taylor (1993)—and we place the two orders in the class Ginkgoopsida.

Intergeneric comparison (Gondwana Triassic)
For discussion, see under *Matatiella* (p. 172).



Reconstructions

The reconstructions of the four of the five Molteno *Peltaspermum* species that occur in our collection are based largely on their respective holotypes. In contrast to many other ovuliferous genera such as the bennettitopsids *Fredlindia* and *Lindtheca*, relatively little interpretation has been necessary. *Peltaspermum* is already well known through studies by Harris (1932a) and Townrow (1960) and excellent specimens are at hand. We have assumed a gently arching, pendulous form of the strobilus for three of the species and an erect mode for *P. tridiscum*, with its robust, zigzag axis.

Evidence for affiliation of organs

The affiliation between *Peltaspermum* and *Lepidopteris* has long been accepted without question—supported by numerous instances of mutual occurrence—throughout their range in Gondwana and Laurasia.

The link is confirmed by Molteno data (Tab. 40), although there are interesting discrepancies in occurrence patterns. All but one of the 17 *Peltaspermum*-yielding TCs also yield *Lepidopteris* (known from 30 of the 100 Molteno TCs); yet *Peltaspermum* occurs in only one of the five Molteno TCs (Aas 411) where *Lepidopteris* exceeds 1% of the foliage assemblage.

Peltaspermales beyond Gondwana Triassic

Laurasian Rhaeto-Liassic—Peltaspermum, with its familiar affiliates *Antevsia* and *Lepidopteris*, occurs widely (e.g. Greenland, Germany, Sweden, Russia) in the Rhaeto-Liassic of Laurasia. It was first recorded by Harris (1932a) and later described in Harris (1937).

Laurasian Permian—Peltaspermum-like megasporophylls occur in the Upper Permian *Tatarian*-Flora of the Russian Platform, where they are placed in separate genera such as *Peltaspermopsis* and *Lopadiangium* (Gomankov & Meyen 1986). Some of these are affiliated with leaves, e.g. *Tatarina*, which are very different from *Lepidopteris*. *Peltaspermum* megasporophylls from the Zechstein Flora of Western and Central Europe were revised by Poort & Kerp (1990) and affiliated with *Lepidopteris* (*Callipteris*)-like leaves.

Molteno occurrence (elaborated)

The five Molteno *Peltaspermum* species recognised here are very distinctive and display an interesting pattern of distribution in the formation. Only *P. monodiscum* is widespread, while the remaining taxa appear restricted to particular habitats. This type of pattern, with one possibly plesiomorphic (classical) species of widespread occurrence spawning several derived, apomorphic (mannerist) species of restricted occurrence, is seen also in other gymnospermous reproductive genera (e.g. *Telemachus*, *Dordrechtites*, *Fraxinopsis*) and foliage genera (e.g. *Ginkgoites*) in the Molteno.

P. thomasii—occurs only at Umk 111 (riparian forest) where it was collected by Thomas (1933) and Townrow (1960). We have found no additional material that we can attribute to this species.

P. monodiscum—occurs in 10 of the 17 TCs yielding *Peltaspermum* and would appear to have flourished in or on the periphery of a range of habitats: *Dicroidium* riparian forest (mature and immature), *Dicroidium* open woodland, *Sphenobaiera* closed woodland and *Heidiphyllum* thicket.

P. tridiscum—occurs in three TCs, all representing *Dicroidium* open woodland and all in the extensive cherty horizon of the Konings Kroon/Peninsula district.

P. turbanatum—also occurs in three TCs (notably Bir 111 and Aas 411), but in this case all are floodplain lake deposits representing *Sphenobaiera* closed woodland. Although the species is known only from these deposits, it clearly extended throughout the duration of the Molteno with Aas 411 occurring low in the formation (Cycle 1) and Bir 111 in the upper levels (Cycle 5).

P. quindiscum—is confined to four TCs representing riparian forests (mature and immature) all occurring low in the Indwe Member (Cycle 2) of the formation.

Gondwana Triassic occurrence (elaborated)

While *Peltaspermum* is relatively frequent and common in the Molteno and the affiliated foliage (*Lepidopteris*) occurs commonly and widespread throughout Gondwana, the ovulate organ remains enigmatically rare outside South Africa. Only three records (very fragmentary material) from Australia and two from South America are known. This extreme rarity is difficult to explain through the lack of intensive or extensive sampling alone.

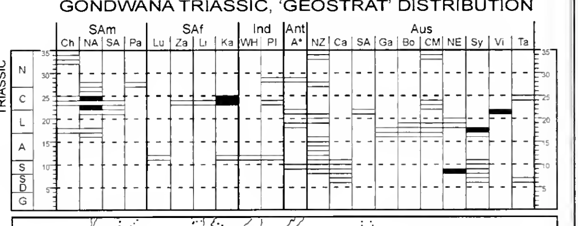
South America

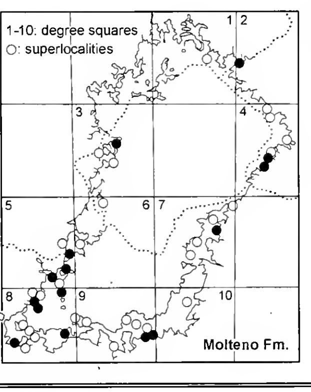
Peltaspermum was first recorded from South America by Baldoni & De Cabrera (1977), who illustrated a single disc from the Portezuelo Fm., and subsequently by Zamuner *et al.* (1999), who figured a fragmentary strobilus from the Cortaderita Fm. Neither specimen is sufficiently preserved for identification to species.

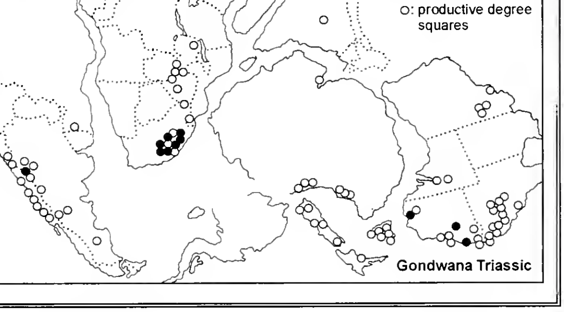
Australia

The three records of *Peltaspermum* from Australia are all of single dissociated megasporophyll discs. They are from three well-separated depositional areas: Bald Hill in Victoria (Douglas 1973); the Lorne Basin in New South Wales (Holmes & Ash 1979); and the Dubbo district of the Great Artesian Basin also in New South Wales (Holmes 1982). The material is inadequate for specific identification.

GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION







Tab. 39.

PELTASPERMUM HYPODIGM, Gondwana Triassic occurrence

AUTHOR		SUBREGION		FORMATION		LOCALITY	NAME	Indivs	ILLUSTRATION	Species: Molteno: *P. thomasii*	*P. monodiscum*	*P. tridiscum*	*P. turbanatum*	*P. quindiscum*	*P. spp. indet*	Intactness: Intact strobili	Fragmentary "	Isolated megasp.
SOUTH AMERICA																		
1977	Baldoni & De C.	Barreal	NA2	25	Portezuelo Fm	Ao. Panul	*Antevsia* sp.	1	pl 1(1)	-	-	-	-	-	1	-	-	1
1999	Zamuner *et al.*	"	"	23	Cortaderita	Level 2	*Peltaspermum* sp.	1	pl 4(C,D)	-	-	-	-	-	1	-	1	-
SOUTH AFRICA																		
1933	Thomas	Elliot	Ka9	24	Molteno	Konings Kroon	*Pteruchus edwardsi*	1	tf 42, pl 24(74)	-	-	-	-	-	1	1	-	-
"	"	Underberg	Ka4	"	"	Umkomaas	*Lepidopteris natalensis*	1	tf 55, pl 24(78)	1	-	-	-	-	-	1	-	-
1955	" (specimen repeated from Thomas 1933)							*	tf 1A	*	-	-	-	-	-	*	-	-
1960	Townrow	Underberg	Ka4	24	Molteno	Umkomaas	*Peltaspermum thomasi*	3	tf 10(B-F), 11(A,B), pl 58(2,8)	3	-	-	-	-	-	3	-	-
1978-1999: And. & And. Molteno literature not included in this table																		
AUSTRALIA																		
1973	Douglas	Victoria	Vi2	22	?	Bald Hill	*Phyllotheca?* sp.	1	pl 14(3)	-	-	-	-	-	1	-	-	1
1979	Holmes & Ash	Lorne B	NE2	9	Camden Head	Camden Head (1583)	circular ribbed object	1	pl 3(8)	-	-	-	-	-	1	-	-	1
1982	Holmes	Dubbo	Sy1	18	(unnamed)	Benolong (Ugothery)	*Peltaspermum*	1	pl 8(E,F)	-	-	-	-	-	1	-	-	1
1986	White (specimen repeated from Holmes 1982)							*	ph on p 153(232)	-	-	-	-	-	*	-	-	*

assemblages (taphocoenosis)		Genera: *Lepidopteris*	♀ *Peltaspermum*	♂ *Antevsia*	Species: *P. monodiscum*	*P. tridiscum*	*P. turbanatum*	*P. quindiscum*	Intactness: Intact strobili	Fragmentary strobili	Isolated discs	Molteno Cycles
Cal 111	Dic/Sph	**5**	-	-	-	-	-	-	-	-	-	
Bir 211	Sph 2spp	-	1	-	-	-	1	-	-	-	1	5
" 111	" "	70	67	-	57	-	10	-	8	4	55	
Boe 111	Lep sto	**90**	-	-	-	-	-	-	-	-	-	4/5
Tel 111	Hei elo	**1**	14	-	14	-	-	-	4	5	5	
Ela 111	Dic odo	5	3	-	3	-	-	-	3	-	-	
Kra 111	Dic odo	10	1	-	1	-	-	-	1	-	-	3
Lut 311	Hei elo	19	7	-	7	-	-	-	-	2	5	
Tin 121	Sph 2spp	1	-	-	-	-	-	-	-	-	-	
Wal 111	Dic odo	2	-	-	-	-	-	-	-	-	-	2/3
Kon 223	Dic odo	4	-	-	-	-	-	-	-	-	-	
" 222	" "	9	24	2	-	24	-	-	8	5	11	
" 111	" "	24	2	-	-	2	-	-	2	-	-	2f
Pen 321	Dic/Ris	9	1	-	-	1	-	-	1	-	-	
" 421	Dic odo	1	-	-	-	-	-	-	-	-	-	
Kle 111	Hei/Dic	**1**	5	-	5	-	-	-	1	2	2	
Kap 111	Dic/Ris	2	1	-	1	-	-	-	-	1	-	2e
Mak 111	Dic odo	7	-	-	-	-	-	-	-	-	-	
Maz 111	Dic cra	2	-	-	-	-	-	-	-	-	-	2c
" 211	Hei/Dic	**1**	9	18	9	-	-	-	-	-	9	
Hla 211	Dic 3spp	**1**	-	-	-	-	-	-	-	-	-	
" 212	Dic 3spp	**1**	-	-	-	-	-	-	-	-	-	
" 213	Dic elo	**1**	-	-	-	-	-	-	-	-	-	2b
Umk 111	Dic 2spp	**1**	17	7	-	-	-	17	3	1	13	
San 111	Dic cra	**1**	2	1	-	-	-	2	-	1	1	
Mat 111	Dic dub	**1**	4	-	-	-	-	4	-	1	3	
Lit 111	Dic/Hei	**1**	11	4	10	-	-	1	4	-	7	2a
Aas 411	Dic/Sph	**7**	88	-	5	-	83	-	22	16	50	
" 511	Dic elo	**10**	-	-	-	-	-	-	-	-	-	1
Ask 111	Equ sp	**20**	-	-	-	-	-	-	-	-	-	
Bam 111	Dic dub	1	-	-	-	-	-	-	-	-	-	
Total TCs		30	17	5	10	3	3	4	11	10	12	
Total indivs		%	257	32	112	27	94	24	57	38	162	

Tab. 40. *Peltaspermum*/*Lepidopteris*, Molteno occurrence, emphasizing stratigraphy (cycles, members)

assemblages (taphocoenosis)		Genera: *Lepidopteris*	♀ *Peltaspermum*	♂ *Antevsia*	Species: *P. monodiscum*	*P. tridiscum*	*P. turbanatum*	*P. quindiscum*	Intactness: Intact strobili	Fragmentary strobili	Isolated discs	Habitat
Umk 111	Dic 2spp	**1**	17	7	-	-	-	17	3	1	13	D1
Lit 111	Dic/Hei	**1**	11	4	10	-	-	1	4	-	7	
Hla 213	Dic elo	**1**	-	-	-	-	-	-	-	-	-	
" 212	Dic 3spp	**1**	-	-	-	-	-	-	-	-	-	
" 211	Dic 3spp	**1**	-	-	-	-	-	-	-	-	-	
Mat 111	Dic dub	**1**	4	-	-	-	-	4	-	1	3	D2
Maz 111	Dic cra	2	-	-	-	-	-	-	-	-	-	
" 211	Hei/Dic	**1**	9	18	9	-	-	-	-	-	9	
Kap 111	Dic/Ris	2	1	-	1	-	-	-	-	1	-	
San 111	Dic cra	**1**	2	1	-	-	-	2	-	1	1	
Kon 222	Dic odo	9	24	2	-	24	-	-	8	5	11	
" 223	" "	4	-	-	-	-	-	-	-	-	-	
" 111	" "	24	2	-	-	2	-	-	2	-	-	
Pen 321	Dic/Ris	9	1	-	-	1	-	-	1	-	-	
" 421	Dic odo	1	-	-	-	-	-	-	-	-	-	D3
Ela 111	" "	5	3	-	3	-	-	-	3	-	-	
Kra 111	" "	10	1	-	1	-	-	-	1	-	-	
Mak 111	" "	7	-	-	-	-	-	-	-	-	-	
Bam 111	Dic dub	1	-	-	-	-	-	-	-	-	-	
Cal 111	Dic/Sph	**5**	-	-	-	-	-	-	-	-	-	
Wal 111	Dic odo	2	-	-	-	-	-	-	-	-	-	
Aas 411	Dic/Sph	**7**	88	-	5	-	83	-	22	16	50	
" 511	Dic elo	**10**	-	-	-	-	-	-	-	-	-	S
Bir 111	Sph 2spp	70	67	-	57	-	10	-	8	4	55	
" 211	" "	-	1	-	-	-	1	-	-	-	1	
Tin 121	" "	1	-	-	-	-	-	-	-	-	-	
Lut 311	Hei elo	19	7	-	7	-	-	-	-	2	5	
Tel 111	" "	**1**	14	-	14	-	-	-	4	5	5	H
Kle 111	Hei/Dic	**1**	5	-	5	-	-	-	1	2	2	
Ask 111	Equ sp	**20**	-	-	-	-	-	-	-	-	-	E
Boe 111	Lep sto	**90**	-	-	-	-	-	-	-	-	-	?
Total TCs		30	17	5	10	3	3	4	11	10	12	
Total indivs		%	257	32	112	27	94	24	57	38	162	

Tab. 41. *Peltaspermum*/*Lepidopteris*, Molteno occurrence, emphasizing ecozones (habitat)

Habitat codes: see tab. 47

Intactness and preservation of cones

Degree of cone fragmentation

Of 257 *Peltaspermum* individuals in our Molteno collection, 57 consist of more or less intact strobili, 38 are fragmentary strobili and the remaining 162 isolated dehisced discs (Tabs 40, 41). Recorded as relative percentages, the three categories rate as 23% intact, 15% fragmentary, 62% dehisced discs. We have nowhere attempted, on site, to estimate the relative percentages of intact individuals as preserved, but since our sampling bias has strongly favoured the more completely preserved material, the figure might be as low as 5 or 10%. This would be comparable, for instance, to *Telemachus*.

Habitat bias

A particularly high proportion of intact strobili occur in the *Dicroidium* open woodland habitat, most notably in the case of *P. tridiscum* in the widespread cherty beds of the Konings Kroon/Peninsula district (D3 in Tab. 41). The most likely conclusion, perhaps, is that these plants grew relatively near to the sites of deposition and were deposited under moderate flow conditions. At the other end of the scale, though *Lepidopteris* foliage occurs regularly at around 1% of the assemblage in the immature *Dicroidium* riparian forest TCs, intact *Peltaspermum* strobili are absent in these sites (D2 in Tab. 41).

In situ *seeds*

Following the pattern observed in *Telemachus*, the great majority of *Peltaspermum* strobili, whether intact or fragmentary, have lost their seeds. Rare specimens with *in situ* seeds have been recovered from Kon 222, pl. 40(1–4) and Umk 111, pl. 44(2, 5).

Dispersed seeds

The typical elongated tetrahedral seeds with bifid tips occur commonly in several TCs, particularly Aas 411, pl. 41(6, 7), pl. 42(6–8). We have not attempted to systematically tabulate their occurrence.

Species nomenclature in *Peltaspermum*

The uncertainties associated with species nomenclature must be addressed in naming the four clearly defined species that we recognise in our Molteno collections. The problem is that the holotypes nominated in Thomas (1933, 1955), Harris (1937) and Townrow (1960) often do not show the diagnostic features that are available to us in our far more extensive and often better preserved collections.

Pteruchus edwardsii Thomas (1933), later described as *Stachyopitys edwardsii* (Thomas) Townrow (1960), was based on a single intact strobilus from Konings Kroon. It is probably a *Peltaspermum*. It is uncertain from which of our TCs in the region the material of Thomas may have been collected. The specimen apparently has simple megasporophylls bearing single discs, not three as in our Konings Kroon palaeodemes. As the preservation is insufficient to make comparisons with our material, we here regard Thomas's material as *Peltaspermum* sp. indet.

Lepidopteris natalenisis Thomas (1933) was instituted by Thomas for a partial, intact inflorescence from his 'Burnera Waterfall locality' (our Umk 111). The collections made by Thomas are housed in the Natural History Museum, London. That specimen was renamed *Peltaspermum thomasii* by Harris (1937) who provided a diagnosis, but no illustrations. The type and two other specimens show simple megasporophylls bearing single discs. From Umk 111, we have collected only intact specimens with compound megasporophylls or diagnostic dehisced discs falling in the species *P. quindiscum*.

P. thomasii is retained as a distinct species. It is closest to *P. monodiscum* in that both bear single discs. The discs of *P. monodiscum* differ from those of *P. thomasii* in the deeply dissected and more numerous lobes. For *P. thomasii*, Townrow (1960) recorded two seeds per disc, but there is probably one seed per lobe as in *P. rotula* from Greenland and in our new Molteno species.

Poort & Kemp (1990) created the new 'natural genus' (their term) *Meyenopteris* for the megasporophyll *Peltaspermum thomasii* plus the leaf *Lepidopteris stormbergensis* (*natalensis*). We see no advantage in using their name at present. They also defined the megasporophyll as bearing only two ovules and being bilaterally symmetrical, while our specimens are clearly multi-ovulate and radially symmetrical.

Adaptive radiation (Molteno diversity)

Diversification in the *Peltaspermum*/*Lepidopteris* plant is most evidently expressed in the female strobilus, with five species described from the Molteno. This contrasts markedly with the male affiliate, *Antevsia*, with only one species recognised. The diagnostic characters defining the species are the number of peltate discs (1 to 5) per megasporophyll; the number, shape, degree of division, ornamentation and attachment of the lobes; and the prominence and shape of the apical cap.

At least five species can be differentiated, four from *Dicroidium*-dominated habitats and one from a *Sphenobaiera* closed woodland habitat. They are based on the following TCs/reference palaeodemes:

P. thomasii—Umk 111 Dic 2 spp (Umkomaas Valley), 3 indivs
Dicroidium riparian forest (mature); Cycle 2b (Indwe Member)
P. monodiscum—Mor 111 Dic odo (Morija) 50 indivs
Dicroidium open woodland (floodplain); Cycle 2c (Indwe Member)
P. tridiscum—Lit 111 Dic/Hei (Little Switzerland) 15 indivs
Dicroidium riparian forest (mature); Cycle 2a (Indwe Member)
P. turbanatum—Aas 411 Dic/Sph (Aasvoëlberg), 60 indivs
Sphenobaiera closed woodland (floodplain lake); Cycle 1 (Bamboesberg Member)
P. quindiscum—Umk 111 Dic 2 spp (Umkomaas Valley), >16 indivs
Dicroidium riparian forest (mature); Cycle 2b (Indwe Member)

Peltaspermum thomasii T.M.Harris 1937

Species concept

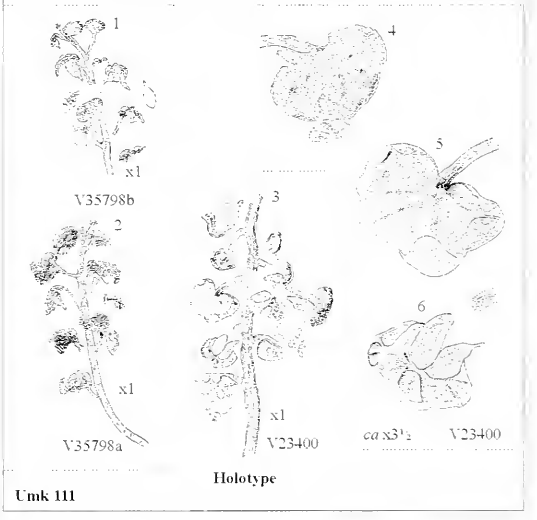
A *Peltaspermum* species with simple megasporophylls bearing undivided discs with *ca* 6 lobes.

Comment & comparison

This species was originally described by Thomas (1933) from Umk 111, later named by Harris (1937) and further described by Townrow (1960).

P. thomasii is distinct from all other *Peltaspermum* species from the Molteno (see generic text for further comment). We have found no further specimens of this species in our particularly extensive collections from the original site (Umk 111).

Peltaspermum thomasii (from Townrow, 1960)



Peltaspermum monodiscum J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/10543; pl. 37(1, 5, 6).
Assemblage (TC): Bir 111 Sph 2spp, Birds River.
Preservation: virtually complete strobilus, without counterpart, with *in situ* seeds in a few discs; impression in thinly laminated, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 57 indivs (7 intact, 1 partial, 49 isolated discs), pl. 37.

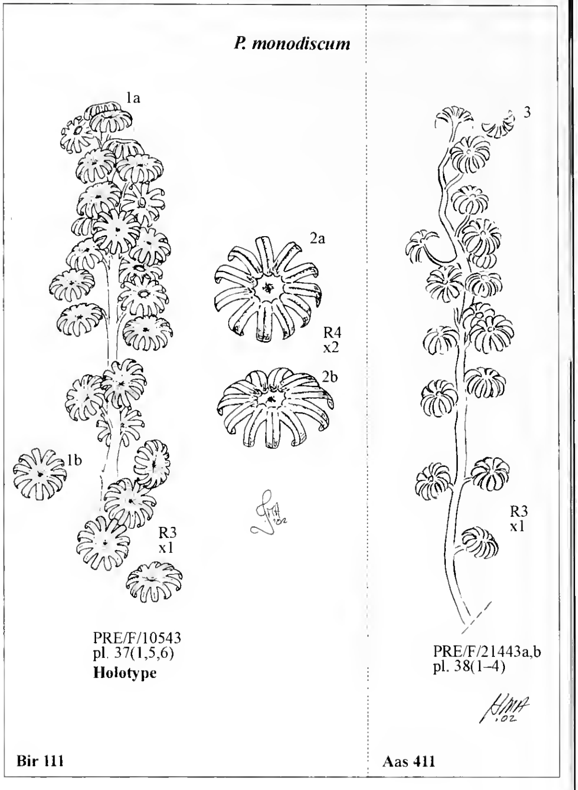
Sister palaeodemes—9 (best 3 listed)
Tel 111 Hei elo: 14 indivs (4 intact, 10 isolated discs).
Lit 111 Dic/Hei: 10 indivs (4 intact, 6 isolated discs).
Aas 411 Dic/Sph: 5 indivs (1 intact, 4 isolated discs), pl. 38(1–4).

Specific diagnosis
A *Peltaspermum* species with simple megasporophylls bearing single deeply divided, linear-lobed discs without cap.

Specific characters
Megasporophyll: simple, bearing a single disc.
Disc: lobes 11 or 12, linear, deeply divided, longitudinally grooved; apical cap not developed.

Etymology
monodiscum—with reference to the single disc per megasporophyll.

Comment & comparison
Represented by 10 palaeodemes in the Molteno, this is the most frequently occurring *Peltaspermum* species in the formation. It is very distinctive and, except for *P. thomasii*, shows no overlap with palaeodemes of other species. Apical caps (which appear clearly in the other three species) have not been observed in *P. monodiscum*.



Peltaspermum tridiscum J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: BP/2/4137a,b; pl. 39(1, 2, 8)
Assemblage (TC): Kon 222 Dic odo, Konings Kroon
Preservation: virtually complete strobilus, part and counterpart, no seeds; clearly preserved; 3D mould and cast in thinly laminated, medium grey cherty shale with poor cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 24 indivs (8 intact, 5 partial, 11 isolated discs), pls 39, 40.

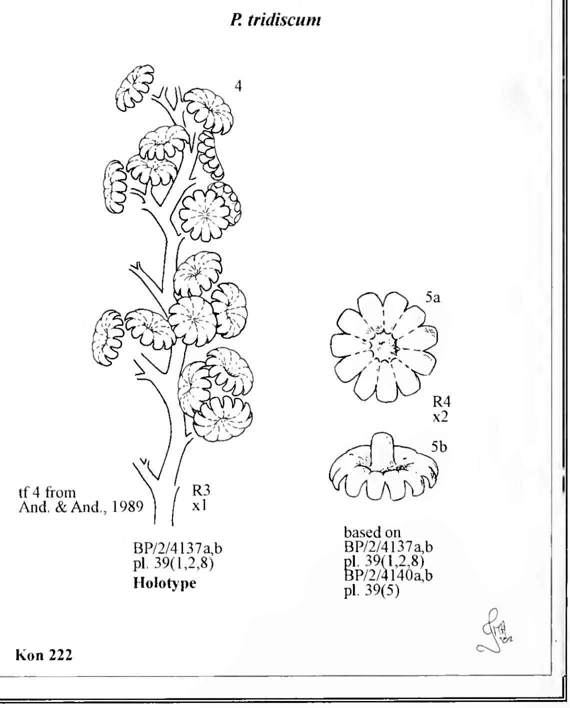
Sister palaeodemes—2 (both listed)
Kon 111 Dic odo: 2 indivs (2 intact).
Pen 321 Dic/Ris: 1 indiv (1 intact).

Specific diagnosis
A *Peltaspermum* species with compound megasporophylls bearing 3 partially divided, roundly lobed discs with cylindrical cap.

Specific characters
Megasporophyll: compound, bearing 3 discs.
Disc: lobes 10 or 11, partially divided, with rounded ends; apical cap cylindrical.

Etymology
tridiscum—with reference to the three discs per megasporophyll.

Comment & comparison
The species is confined to the extensive cherty horizon of the Konings Kroon-Peninsula district, and it is the only member of the genus found in these cherts. Though *P. turbanatum* also has megasporophylls generally bearing three discs, the features of the discs are clearly distinctive. The apical cap is rarely preserved and is best seen—positive and negative—in the two specimens BP/2/4144a,b and BP/2/4140a,b, pl. 39(5). The strobilus axis has a characteristic zig-zag not found in other species.



Peltaspermum turbanatum J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F 21440a,b; pl. 41(1, 2).
Assemblage (TC): Aas 411 Dic/Sph, Aasvoëlberg.
Preservation: virtually complete strobilus, part and counterpart, no *in situ* seeds; impression in thinly laminated, strongly baked, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 83 indivs (21 intact, 16 partial, 46 isolated discs), pls 41, 42.

Sister palaeodemes—2 (best 1 listed)
Bir 111 Sph 2spp: 10 indivs (1 intact, 3 partial, 6 isolated discs), pl. 43(1–6).

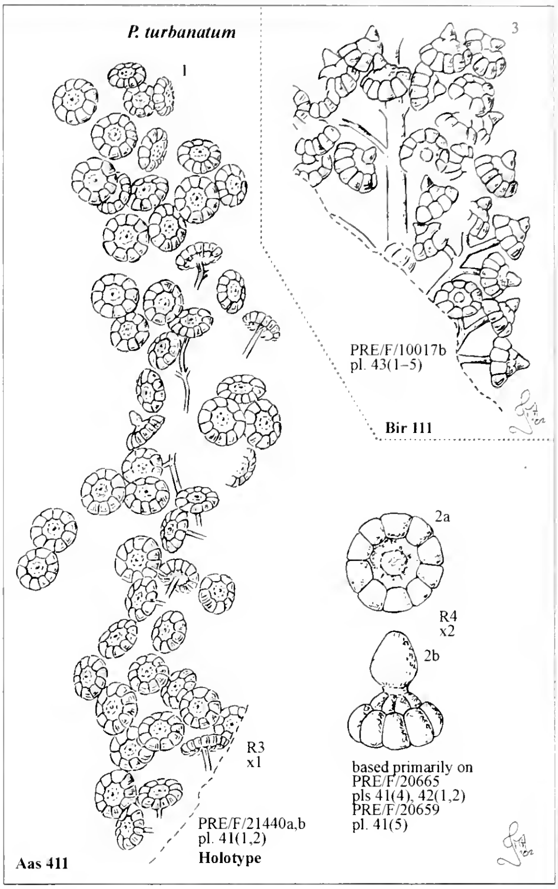
Specific diagnosis
A *Peltaspermum* species with compound megasporophylls bearing 3 or 4 undivided, roundly lobed discs with large turban-like cap.

Specific characters
Megasporophyll: compound, bearing 3 or 4 discs.
Disc: lobes 10, short/stout, not divided or grooved, extending from distinctive concentric collar; apical cap pronounced, turban-like.

Etymology
turbanatum—with reference to the turban-like apical cap.

Comment & comparison
P. turbanatum is restricted to the lake deposits of Aasvoëlberg and Birds River. Though the single intact specimen from Bir 111 (tf. 2) clearly shows at least one megasporophyll bearing four discs—and this may well have been the norm—the features of the individual discs are very like those of Aas 411 and the palaeodeme is therefore included in the same species.

At Aas 411 the isolated tetrahedral seeds [pls 41(6, 7), 42(5, 7, 8)] are very common and occur on most slabs.



Peltaspermum quindiscum J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/18711a,b; pl. 44(1, 2, 4–6).
Assemblage (TC): Umk 111 Dic 2spp, Umkomaas Valley.
Preservation: virtually complete strobilus, part and counterpart, with *in situ* seeds; compression in thinly laminated, carbonaceous (good cuticle), moderately baked, dark grey shale with good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 17 indivs (3 intact, 1 partial, 13 isolated discs), pl. 44.

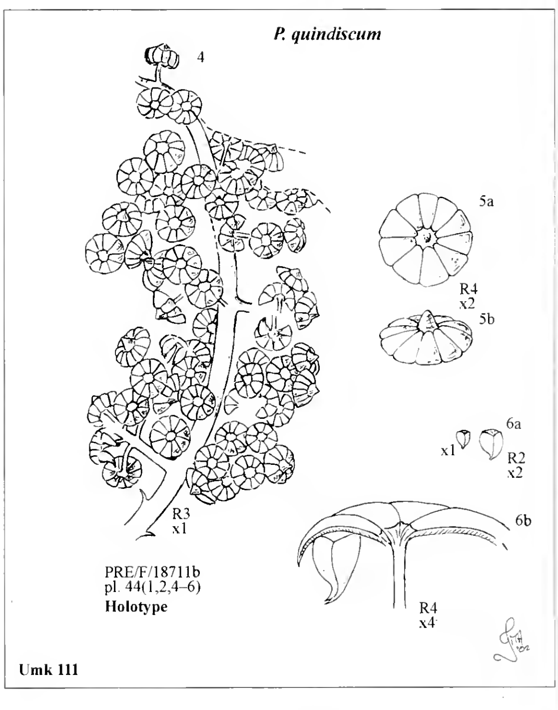
Sister palaeodemes—3 (best 1 listed).
Lit 111 Dic/Hei: 1 indiv. (intact).

Specific diagnosis
A *Peltaspermum* species with compound megasporophylls bearing *ca* 5 undivided, truncate-lobed discs with short conical cap.

Specific characters
Megasporophyll: compound, bearing 5 discs.
Disc: lobes 10, not divided or grooved, truncate; apical cap conical.

Etymology
quindiscum—with reference to the five discs per megasporophyll.

Comment & comparison
P. quindiscum is confined to four palaeodemes representing riparian forests in the lower sections of the Indwe Member. In view of the distinctive nature of the discs, the material (mostly isolated discs) from San 111, Mat 111 and Lit 111 has been placed in the same species as the reference palaeodeme from Umk 111.



Antevsia T.M.Harris 1937

Type species
Antevsia zeilleri (Nath.) T.M.Harris 1937.
Scoresby Sound, E. Greenland; Rhaetic, Triassic.

Generic concept
A ginkgoopsid male strobilus of variously branched form, with linear, planar, simple to branching microsporophylls bearing lateral, sessile clusters of microsporangia.

Generic characters (Molteno Fm.)
Attachment: strobilus borne singly on a bulbous short shoot (which dehisces as a unit).
Strobilus: simple, lax to compact, bushy, radially symmetrical, medium-sized (*ca* 80 x 70 mm); axis erect, tapering; microsporophylls fairly numerous, irregularly helical.
Microsporophyll: simple to irregularly forked or branched, linear, planar, pinnate; bracteoles absent; rhachis robust, with clear distinction into blistered midrib and naked flange; fertile heads numerous, regularly closely spaced, sessile, in opposite to subopposite pairs; microsporangia fascicled to pinnulate, 3–10 per head.
Microsporangium: irregularly elliptic (2–3 mm long); ornamentation fine, linear, sinuous, forking and converging.
Pollen: nonsaccate, monocolpate.

Eponymy
Antevsia—after Dr E. Antevs, a Swedish palaeobotanist who added greatly to the understanding of this genus.

Global range: numerous species, Pangaea, Tr.–J.

Gondwana Triassic occurrence
SAf—Karoo Basin, 5 TCs (33 indivs).
Antevsia appears not to have been previously recorded from elsewhere in the Gondwana Triassic (except incorrectly by Townrow 1960).

Molteno occurrence
Frequency (F): 5 TCs (of 100 sampled in the Molteno).
Diversity (D): 1 species.
Abundance (A): 32 individuals, very rare to extremely rare.

Maz 211 Dic 3spp:	18	indivs	in	85	man-hrs	cleaving	(2	per	1	man-day)	very rare
Kon 222 Dic odo:	1	"	"	40	"	"	(1	"	2	")	"
San 111 Dic cra:	2	"	"	30	"	"	(1	"	1	")	"
Umk 111 Dic 2spp:	7	"	"	400	"	"	(1	"	6	")	extr. rare
Lit 111 Dic/Hei:	4	"	"	550	"	"	(1	"	14	")	"

Antevsia is far less common overall and less frequent than the female affiliate *Peltaspermum*.

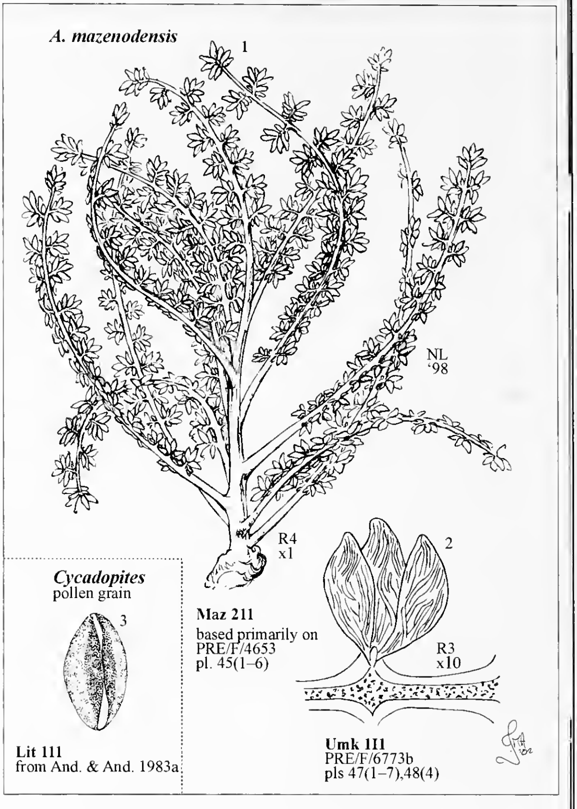
Affiliated organs
Female strobilus: *Peltaspermum*—Grade 3 (Kin. reinf., Mut. occ.).
Foliage: *Lepidopteris*—Grade 3 (Kin. reinf., Mut. occ., Mor. corr.).

Classification & comparison
Suprageneric classification (Peltaspermaceae/Peltaspermales)
See discussion under *Peltaspermum* (p. 148).

Intergeneric comparison (Gondwana Triassic)
Antevsia is close to the genera *Stachyopitys* and *Pteruchus* in that all bear clusters of fairly similar microsporangia. Poorly preserved specimens can easily be confused. However, *Antevsia* has sessile lateral clusters of 3–10 microsporangia; *Pteruchus* is differentiated by the clear laminate head bearing numerous abaxial microsporangia; *Stachyopitys* has numerous microsporangia radiating from a central receptacle.

Townrow (1960), in error, classified *Fanerotheca exstans* as *Antevsia*. Earlier, we followed Townrow and thus ascribed two specimens [And. & And. 1983, pl. 23(3, 4)] to *Antevsia*, which in the present study are reclassified as *Fanerotheca*.

Comparisons beyond Gondwana Triassic
Laurasian Jurassic—The Middle Jurassic genus *Caytonanthus* (Crane 1985), first described from the Yorkshire flora of England, has clusters of microsporangia similar to *Antevsia*. They differ in *Caytonanthus* bearing multiloculate sporangia and *Antevsia* simple sporangia.
Laurasian Permian—The Upper Permian (Tatarina Flora, Russian Platform) genus *Permotheca*, placed in the order Peltaspermales by Gomankov & Meyen (1986), has clusters of simple microsporangia similar to *Antevsia*. The pollen is recorded as disaccate by Meyen (1987, fig. 78d).



Reconstructions
The R4 reconstruction of *A. mazenodensis* (tf. 1 above), with many unbranched microsporophylls angling steeply upwards from the central axis, is based on the holotype (Maz 211, PRE/F/4653). The only other reasonably sized portion of a strobilus (Maz 211, PRE/F/11729), intact except for the base, shows a far more complex branching pattern of the microsporophylls. A fascicle of three sporangia (Umk 111, PRE/F/6773) is illustrated in tf. 2.

The curious reconstruction of a *Lepidopteris* leaf with an *Antevsia*-like strobilus attached to the distal extremity of the midrib was illustrated in Taylor & Taylor (1993, fig.15.31). This was based on two specimens collected by Zavada (pers. comm., 1994) from Umkomaas Valley. As we have never observed anything similar, we await a published description of this unique find.

Evidence for affiliation of organs
Compared to the female strobilus *Peltaspermum*, the male, *Antevsia*, is rare in the Molteno and co-occurs with *Lepidopteris* in only five TCs (Tab. 42). The affiliation of *Antevsia* with the female fruit *Peltaspermum* and the foliage genus *Lepidopteris* merits Grade 3 reliability. This is supported by the Laurasian evidence given below.

Mutual occurrence
Antevsia is found only in Cycle-2 of the Molteno and almost exclusively (four of five appearances) in TCs associated with *Dicroidium* riparian forests (Tabs 40–42). In these Cycle-2 TCs the correspondence of occurrence between *Antevsia* and *Peltaspermum* is near perfect, while elsewhere in the Molteno the correspondence is almost nil. This discrepancy may be explained by postulating differing seasons of maturation for the male and female fruit.

Morphological correspondence
The *Antevsia* specimens from Umk 111 (most notably PRE/F/6773, tf. 2 above) show the same distinctive blistering of the midrib that is found in *Lepidopteris*.

Laurasian evidence
Antevsia occurs with *Lepidopteris* at three Swedish Rhaetic localities (Antevs 1914) and at three Greenland Rhaetic localities (Harris 1932a), where *Peltaspermum* is also present. Both Antevs and Harris have demonstrated the cuticular similarities of the two organs.

assemblages (taphocoenosis)		Genera: *Lepidopteris*	Genera: ♀ *Peltaspermum*	Genera: ♂ *Antevsia*	Intactness: intact strobili	Intactness: partial strobili	Intactness: isolated microsporangia	Molteno Cycles
Call 111	Dic/Sph	5	-	-	-	-	-	5
Bir 211	Sph 2spp	-	1	-	-	-	-	
" 111	" "	70	67	-	-	-	-	
Boe 111	Lep sto	90	-	-	-	-	-	4/5
Tel 111	Hei elo	1	14	-	-	-	-	3
Ela 111	Dic odo	5	3	-	-	-	-	
Kra 111	" "	10	1	-	-	-	-	
Lut 311	Hei elo	19	7	-	-	-	-	
Tin 121	Sph 2spp	1	-	-	-	-	-	
Wal 111	Dic odo	2	-	-	-	-	-	2/3
Kon 223	" "	4	-	-	-	-	-	2f
" 222	" "	9	24	2	-	2	-	
" 111	" "	24	2	-	-	-	-	
Pen 321	Dic/Ris	9	1	-	-	-	-	
" 421	Dic odo	1	-	-	-	-	-	
Kle 111	Hei/Dic	1	5	-	-	-	-	
Kap 111	Dic/Ris	2	1	-	-	-	-	2e
Mak 111	Dic odo	7	-	-	-	-	-	2c
Maz 111	Dic cra	2	-	-	-	-	-	
" 211	Hei/Dic	1	9	18	2	14	2	
Hla 211	Dic 3spp	1	-	-	-	-	-	2b
" 212	" "	1	-	-	-	-	-	
" 213	Dic elo	1	-	-	-	-	-	
Umk 111	Dic 2spp	1	17	7	1	4	2	
San 111	Dic cra	1	2	1	-	1	-	
Mat 111	Dic dub	1	4	-	-	-	-	
Lit 111	Dic/Hei	1	11	4	1	1	2	2a
Aas 411	Dic/Sph	7	88	-	-	-	-	1
" 511	Dic elo	10	-	-	-	-	-	
Ask 111	Equ sp.	20	-	-	-	-	-	
Bam 111	Dic dub	1	-	-	-	-	-	
Total TCs		30	17	5	3	5	3	
Total indivs		%	257	32	4	22	6	

Tab. 42. *Antevsia*, Molteno occurrence

Antevsia mazenodensis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/4653; pl. 45(1–6).
Assemblage (TC): Maz 211 Hei/Dic; Mazenod.
Preservation: almost complete strobilus, without counterpart; compression in thinly laminated, carbonaceous (poor cuticle), medium grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 18 indivs (2 intact, 14 partial, 2 isolated microsporangia), pls 45(1–6), 46(1–7).

Sister palaeodemes—4 (best 1 listed)
Umk 111 Dic 2spp: 7 indivs (1 intact), pls 47, 48.

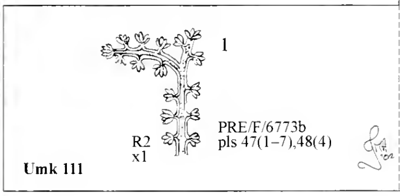
Specific diagnosis
An *Antevsia* species with microsporophylls in opposite fertile heads bearing 3–6 microsporangia.

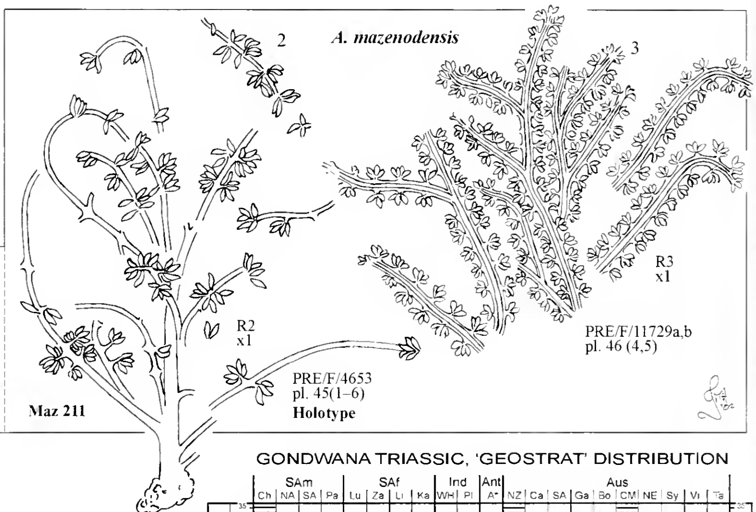
Specific characters: as per genus.

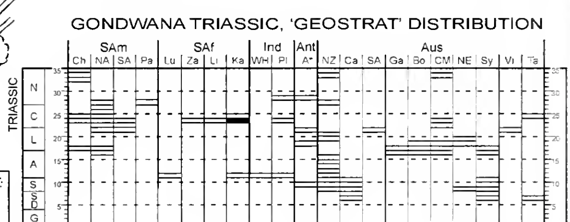
Etymology
mazenodensis—with reference to the type locality.

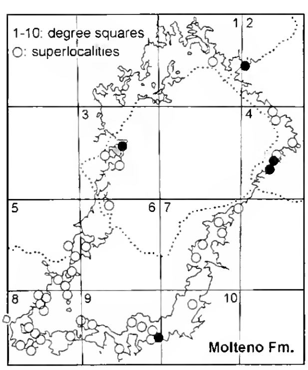
Comment & comparison
From the relatively few Molteno specimens at hand, the *Antevsia* strobilus appears to show a particularly irregular morphological organisation (tfs 1–3 below). In only one specimen (Maz 211, PRE/F/4653, tf. 2 below) is the more or less complete strobilus preserved. It is attached to a bulbous short shoot similar to that seen in many *Stachyopitys* individuals.

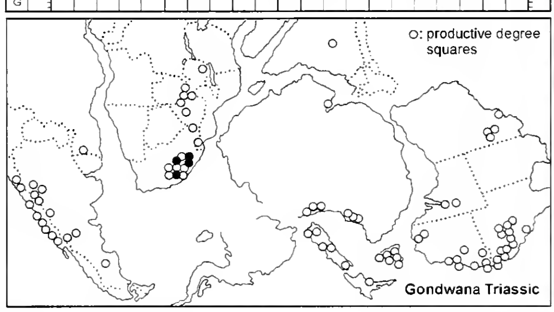
This Molteno species differs from the Laurasian *Antevsia zeilleri*, which bears two or three ultimate fertile heads and clusters of 6–10 microsporangia. While five distinct Molteno species are recognised in the ovulate genus *Peltaspermum*, the present collections are insufficient to attempt to differentiate species within the supposed male affiliate *Antevsia*.











Lepidopteris Schimp. 1869

Type species
Lepidopteris stuttgardiensis (Jaeger 1827) Schimp. 1869.
Near Stuttgart, Germany; Keuper, Triassic.

Generic concept
A ginkgoopsid leaf with robust blistered rhachis, obovate, pinnate to bipinnate lamina and zwischenfiedern.

Generic characters (Molteno Fm.)
Attachment: unknown.
Leaf: pinnate to bipinnate, obovate, medium to large; petiole short stout, rhachis robust with characteristic blisters; pinnae opposite to subopposite, closely spaced, sometimes decurrent, entire to deeply pinnatisect to pinnate, narrowly lanceolate; zwichenfiedern usually present; pinnules (in bipinnate forms) opposite to subopposite, closely spaced, often conjoining and becoming coherent; venation pinnate, lateral veins fine, simple or forking; in coherent forms, sometimes conjoining with veins of adjacent pinnules.
Cuticle: see And. & And. (1989, p. 90); this vol., tfs 1–4 below.

Etymology
Lepidopteris—lepido (Gr.), scaly; *pteris* (Gr.), fern.

Global range: several spp., Pangaea, U.P.–U.Tr.

Gondwana Triassic occurrence (after And. & And. 1989)
Frequency (F): 19 degree squares (of the 84 across Gondwana).
Ubiquity (U): 4 continents (of 5 comprising Gondwana).
Diversity (D): 5 foliage species.
Abundance (A): 1% (the norm in Molteno TCs).
Longevity (L): 21 myrs (Scythian to early Norian).

Colonisation success: FUDAL rating 19/4/5/1/21 = 50.
Intermediate success (Grade 3): *Lepidopteris* was the eighth most prominent genus in the Gondwana Triassic; it was frequent, ubiquitous and long-lived, but of relatively moderate diversity and abundance.

Endemism: of the five described Gondwana Triassic species, three (*L. africana*, *L. stormbergensis* and *L. madagascariensis*) are widespread, while the remaining two (*L. brownii* and *L. langlohensis*), as known, are single-formation endemics.

Molteno occurrence
Frequency (F): 30 TCs (of 100 sampled in the Molteno).
Diversity (D): 2 species.
Abundance (A): monodominant (90%) in 1 TC; co-dominant (20%) in 1 TC; common to abundant (5–10%) in 3 TCs; occasional (1%) in 10 TCs; rare to very rare (<1%) in the other 15 TCs.

Habit: possibly woody, much-branched spreading shrub.
Preferred habitat: ubiquitous in *Dicroidium* riparian forest, less frequent (5 of 10 TCs) in closed woodland of the lake margins.

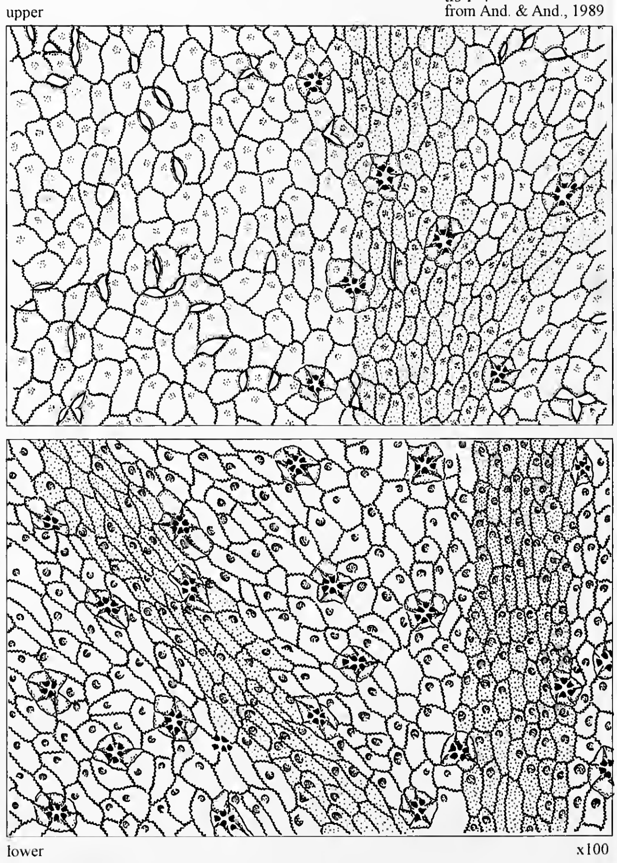
Affiliated organs
Female strobilis: *Peltaspermum*—Grade 4 (Mut. occ., Mor. cor., Cut. cor.).
Male strobilus: *Antevsia*—Grade 3 (Kin. reinf., Mut. occ.).

Classification & comparison

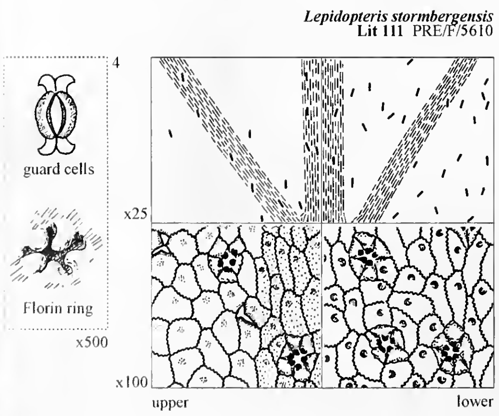
Intergeneric comparisons
Gondwana Triassic—Lepidopteris, as a bipinnate leaf with intercalary pinnules (zwischenfiedern) along the rhachis, is unique amongst the Gondwana ginkgoopsid leaf genera. *Lepidopteris* and the genus *Scytophyllum* are end members of an intergrading range of leaves in which the pinnules coalesce and become coherent. The choice of genus for leaves that are partially coherent is subjective. The cuticular features compare well with those of other ginkgoopsid foliage, and most closely resemble *Dicroidium*. *Lepidopteris* cuticle is well-developed, with notable features such as buttressed cell walls and the ring of subsidiary cells. Where material is sparse or imperfectly preserved, *Lepidopteris* may be confused with fern leaves.

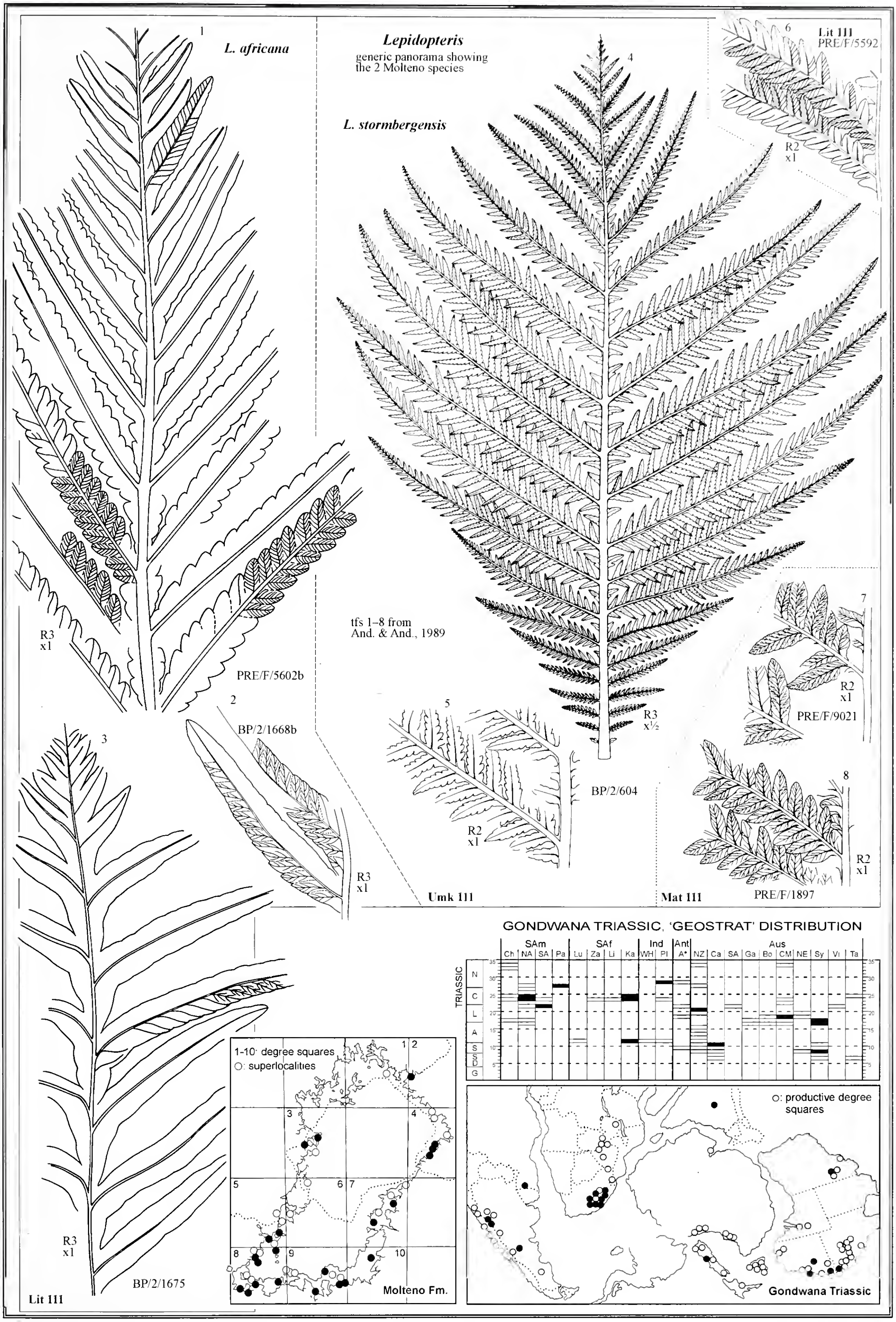
Interspecific comparisons
Of the five Gondwana Triassic species of *Lepidopteris* recognised by us (And. & And. 1989), only *L. stormbergensis* and *L. africana* occur in the Molteno. The two forms are found together in 11 of the 30 Molteno TCs yielding *Lepidopteris*, and in most of these cases they appear to constitute an unbroken morphological range within a single palaeodeme. In the remaining TCs, only one or the other of the species is encountered.

tfs 1–4
from And. & And., 1989



Lepidopteris stormbergensis
Lit 111 PRE/F/5610




L. africana
Lepidopteris
generic panorama showing
the 2 Molteno species
L. stormbergensis
Lit 111
PRE/F/5592
R2
x1
R3
x1
PRE/F/5602b
tfs 1–8 from
And. & And., 1989
R3
x½
R2
x1
PRE/F/9021
BP/2/1668b
BP/2/604
R3
x1
Umk 111
Mat 111
PRE/F/1897
GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION
SAm
SAf
Ind
Ant
Aus
Ch
NA
SA
Pa
Lu
Za
Li
Ka
WH
Pl
A*
NZ
Ca
SA
Ga
Bo
CM
NE
Sy
Vi
Ta
TRIASSIC
N
C
L
A
S
S
D
G
BP/2/1675
Lit 111
1-10 degree squares
○: superlocalities
Molteno Fm.
○: productive degree squares
Gondwana Triassic

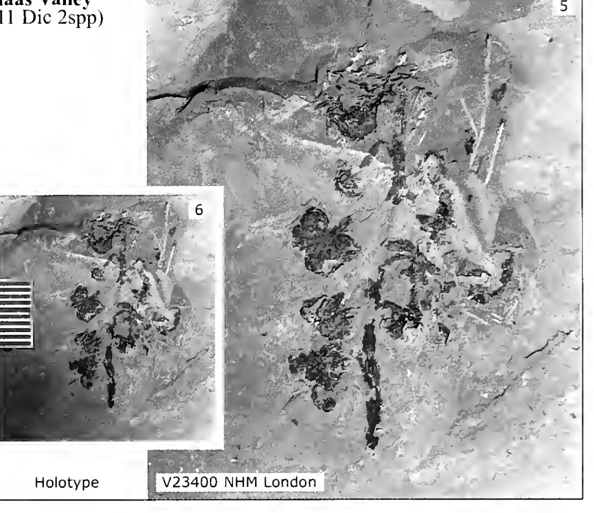
Peltaspermum monodiscum **pl. 37** **PELTASPERMALES**

Aasvoëlberg
(Aas 411 Dic/Sph)

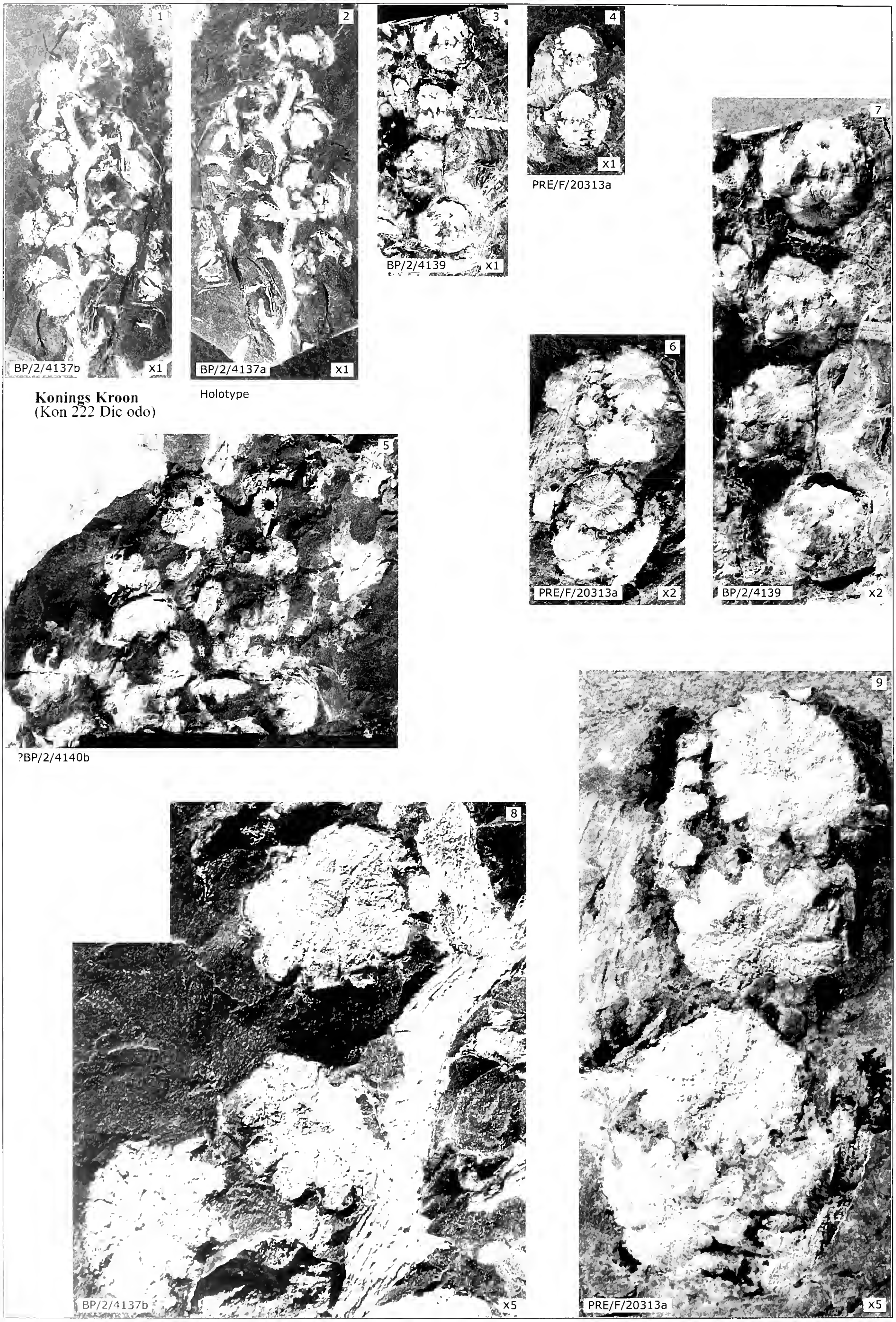
P. monodiscum

P. thomasii

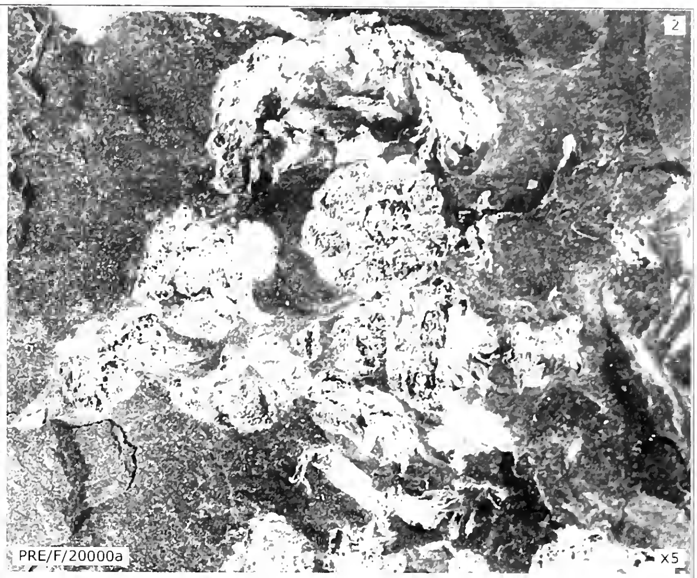
Umkomaas Valley
(Umk 111 Dic 2spp)

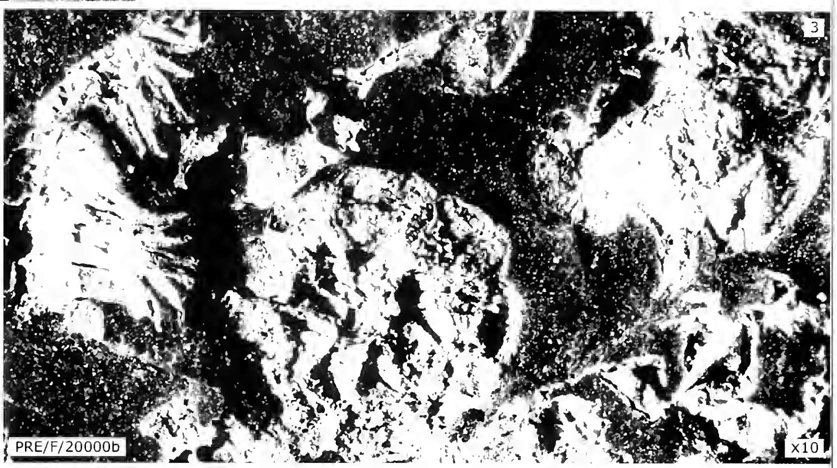


Holotype

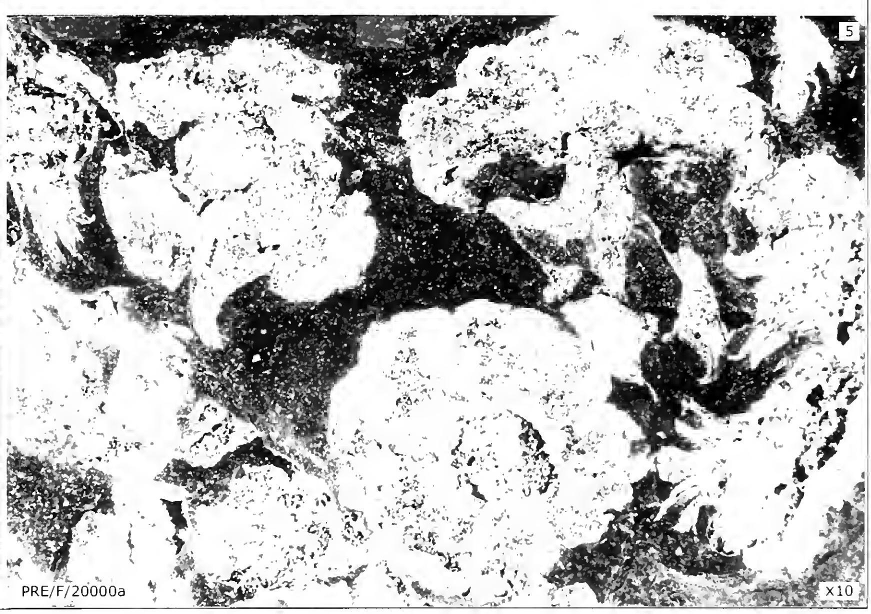


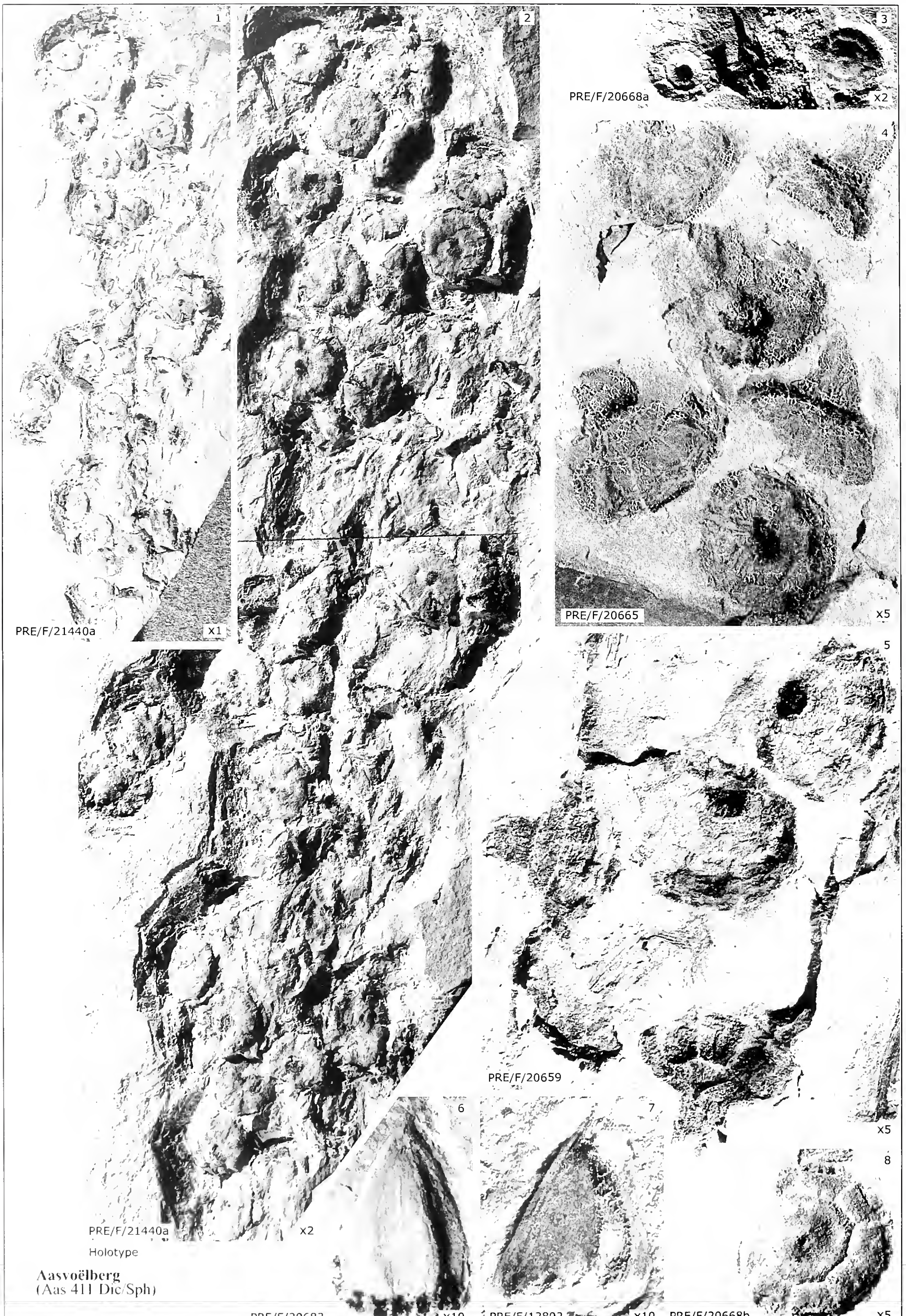
Peltaspermum tridiscum pl. 39

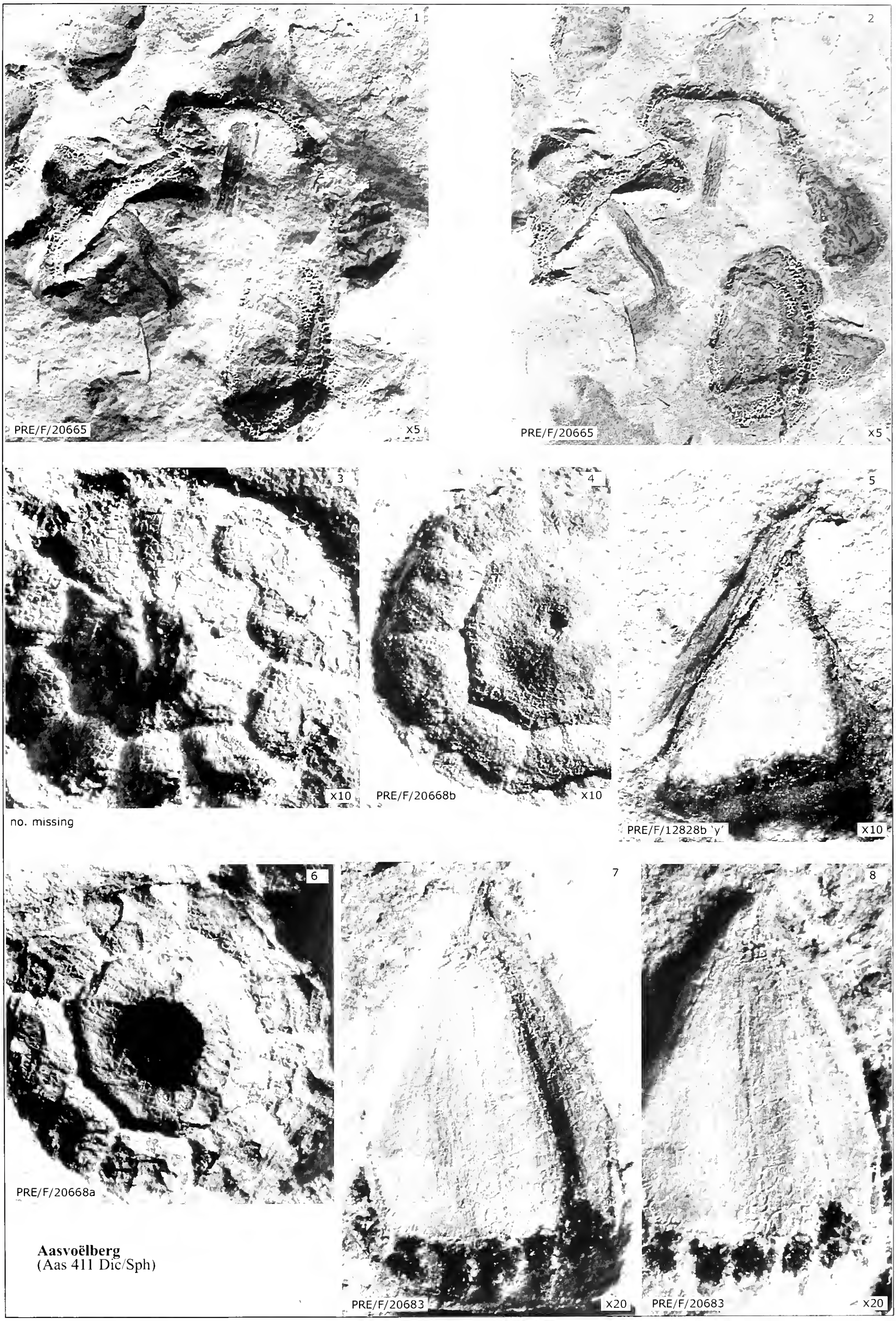




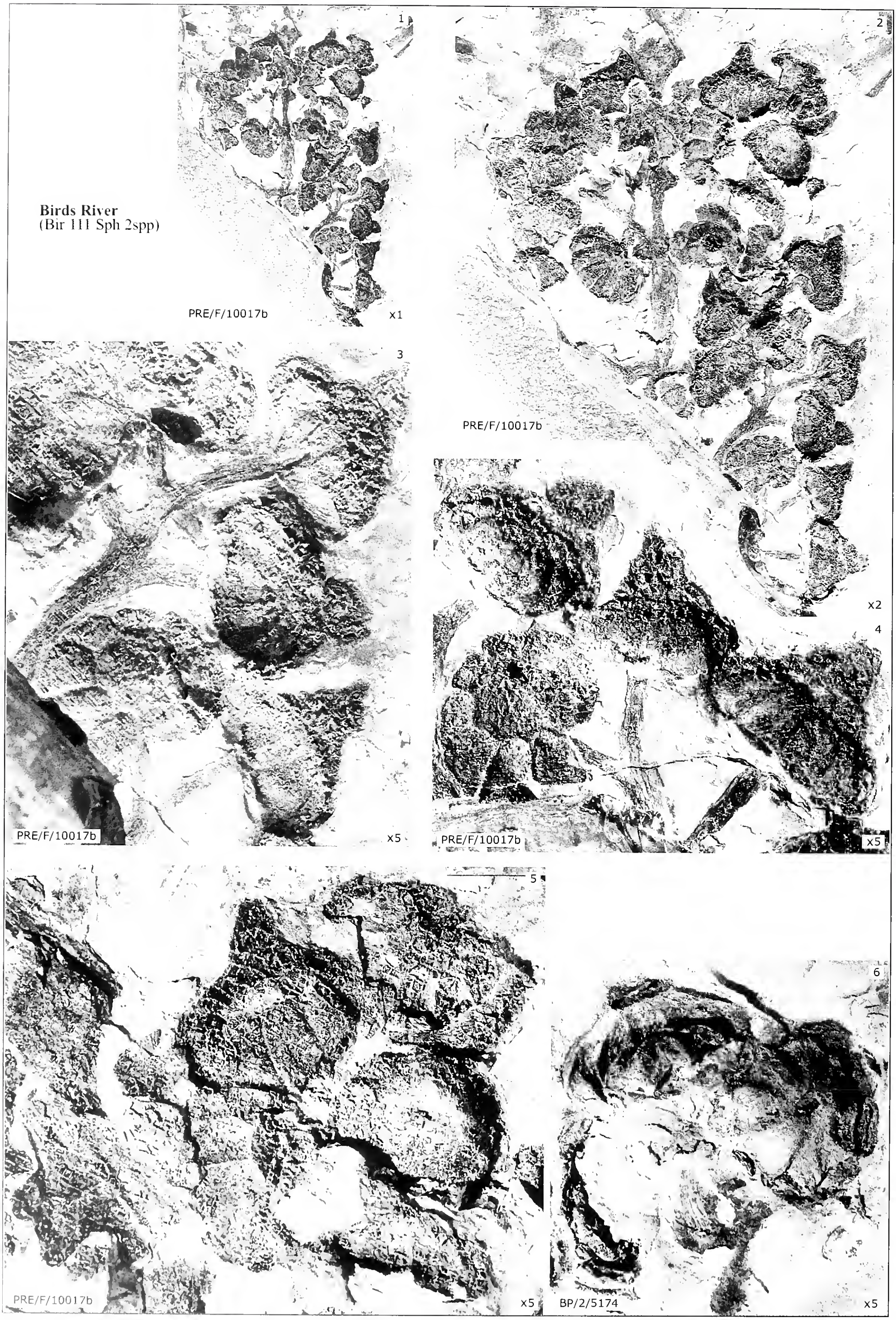
Konings Kroon
(Kon 222 Dic odo)



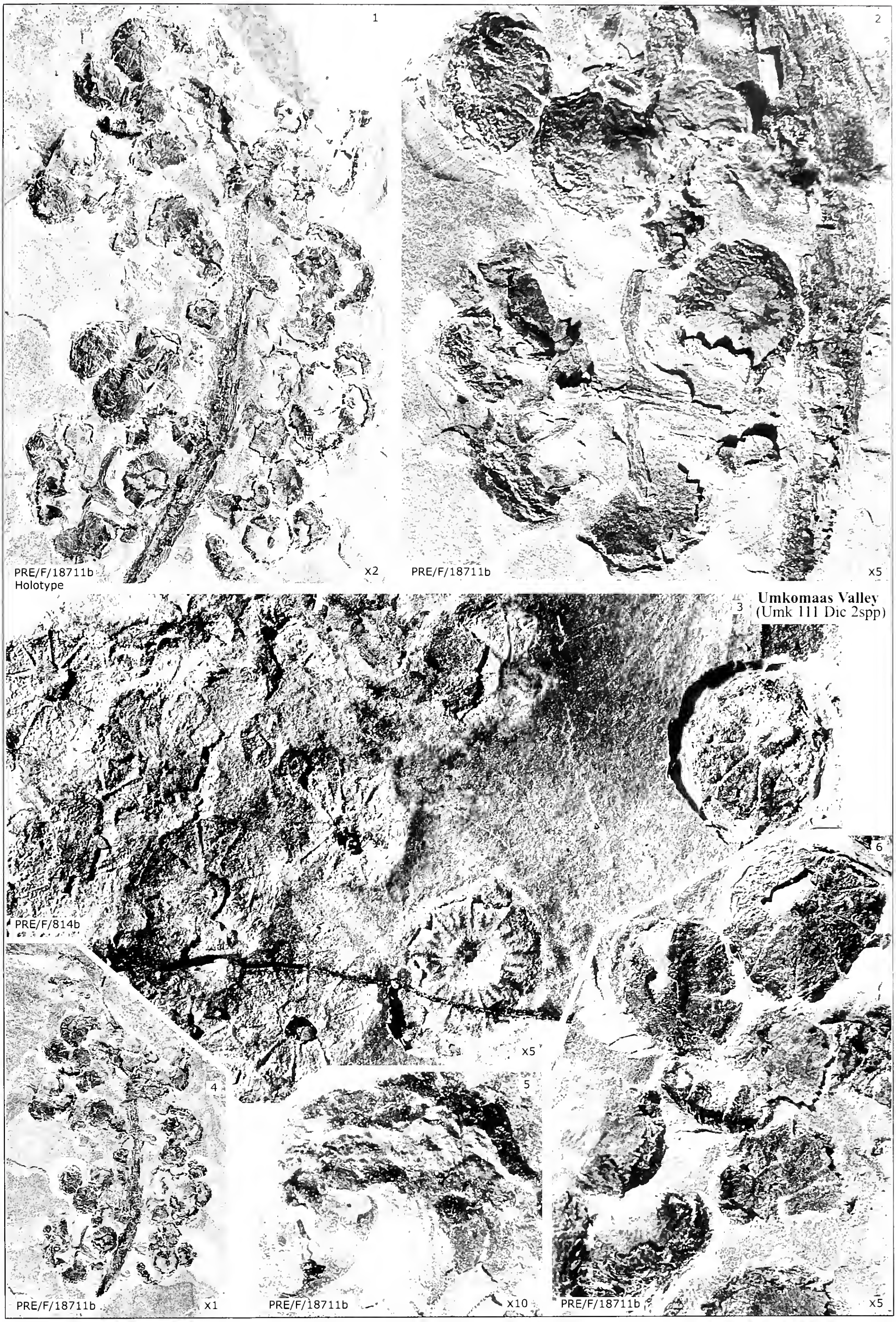

1
2
3
PRE/F/20668a
x2
4
PRE/F/21440a
x1
PRE/F/20665
x5
5
PRE/F/20659
x5
6
7
8
PRE/F/21440a
Holotype
x2
Aasvoëlberg
(Aas 411 Dic/Sph)
PRE/F/20683
x10
PRE/F/12802
x10
PRE/F/20668b
x5



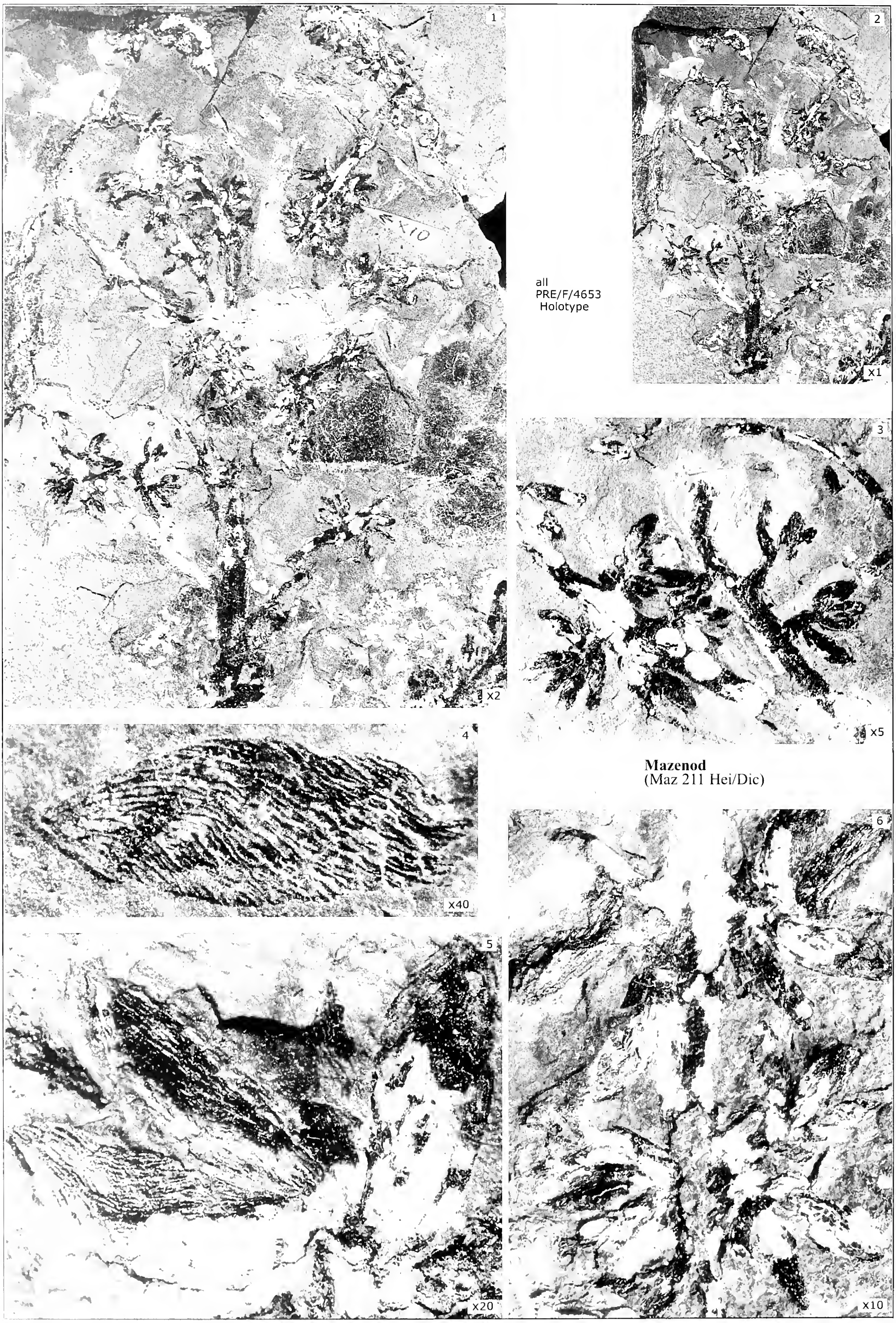
PELTASPERMALES **pl. 42** ***Peltaspermum turbanatum***



Peltaspermum turbanatum pl. 43 PELTASPERMALES

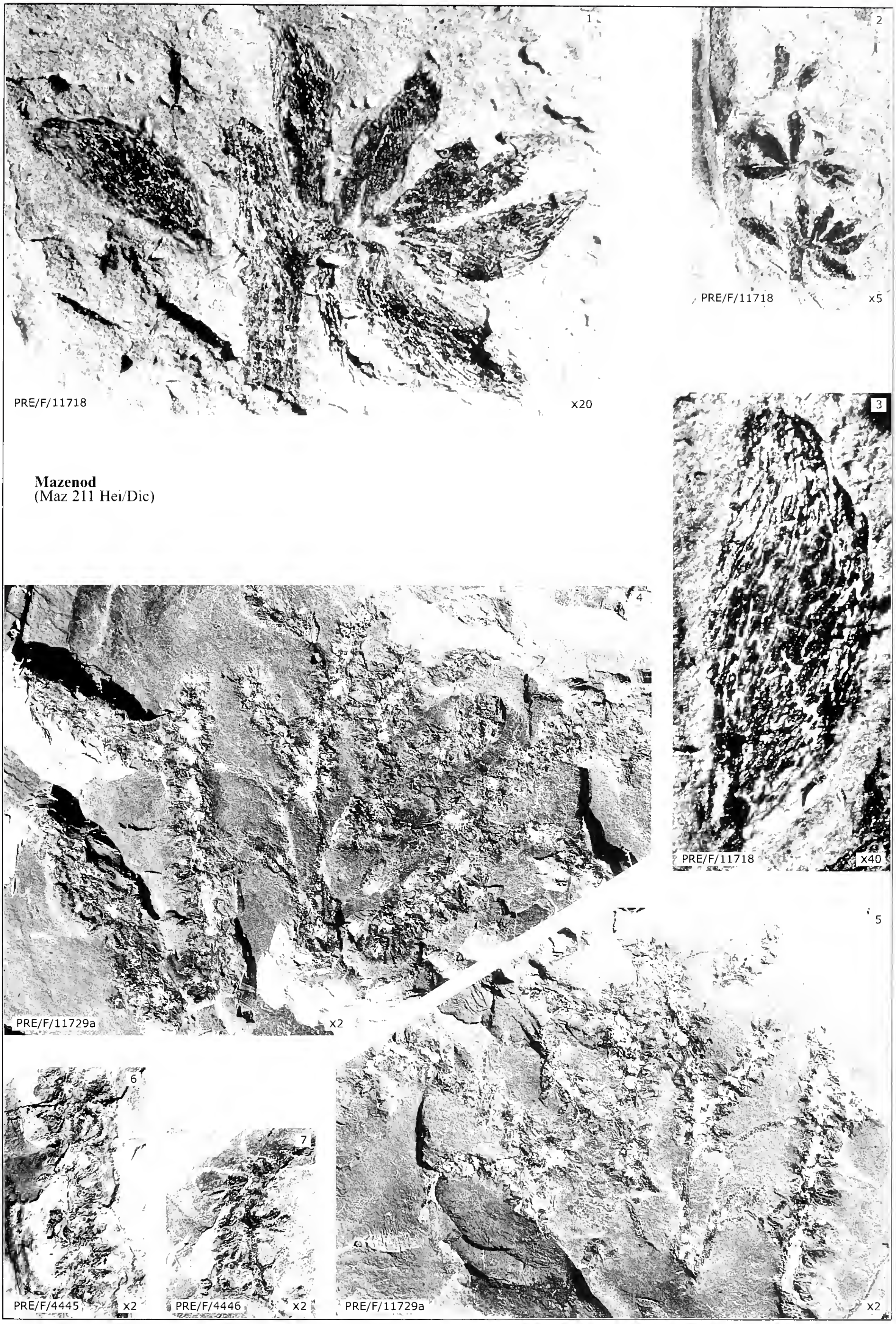


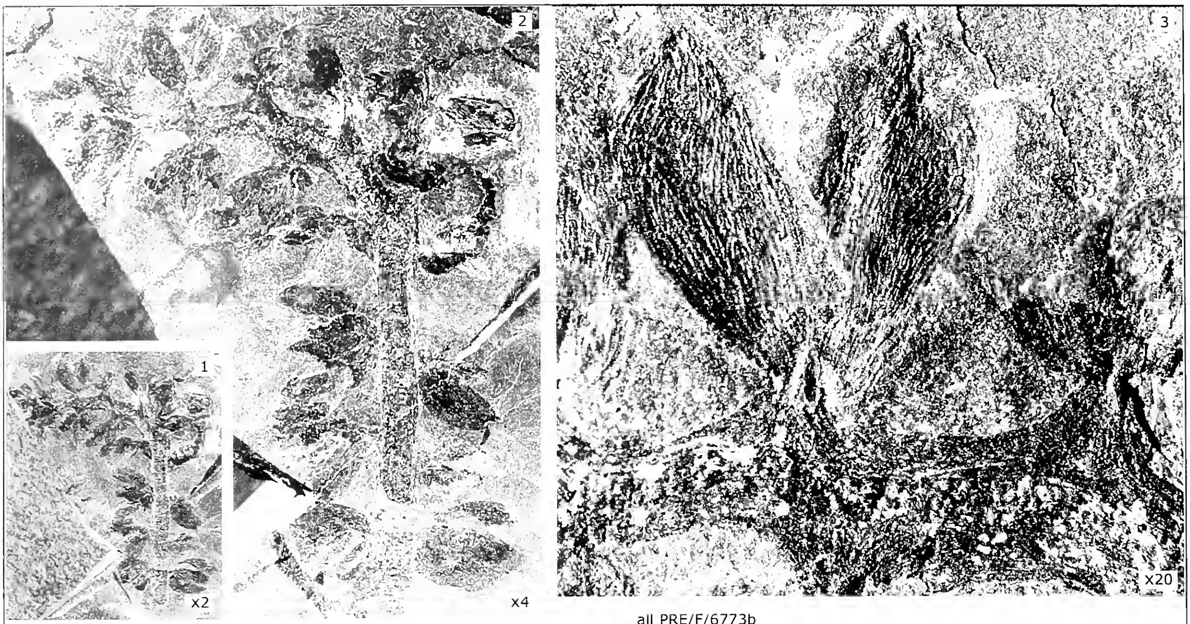
PELTASPERMALES **pl. 44** *Peltaspermum quindiscum*



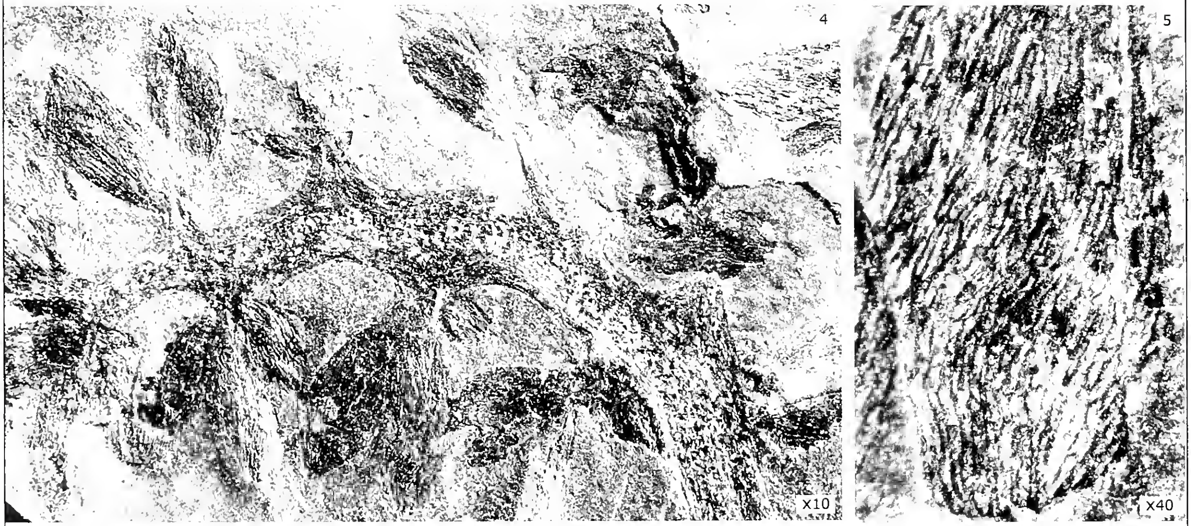
all
PRE/F/4653
Holotype

Mazenod
(Maz 211 Hei/Dic)

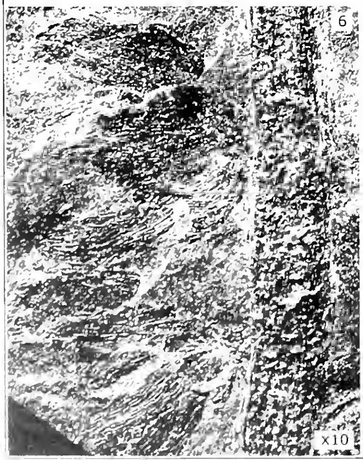

1
PRE/F/11718
x20
2
PRE/F/11718
x5
Mazenod
(Maz 211 Hei/Dic)
3
PRE/F/11718
x40
4
PRE/F/11729a
x2
5
PRE/F/11729a
x2
6
PRE/F/4445
x2
7
PRE/F/4446
x2

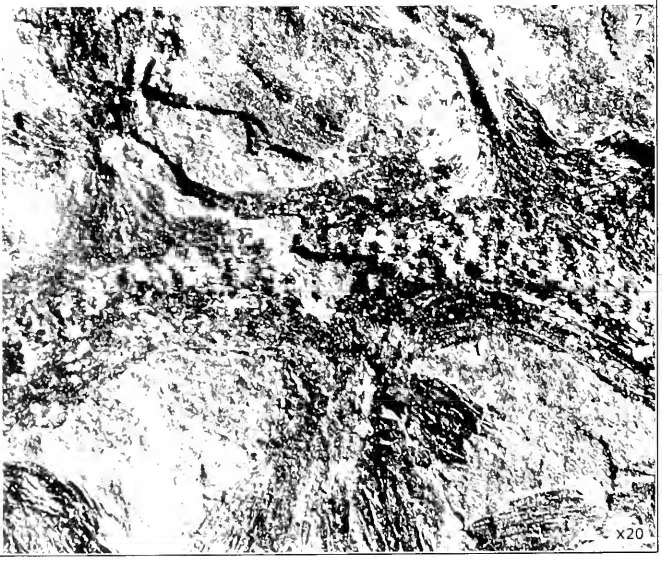


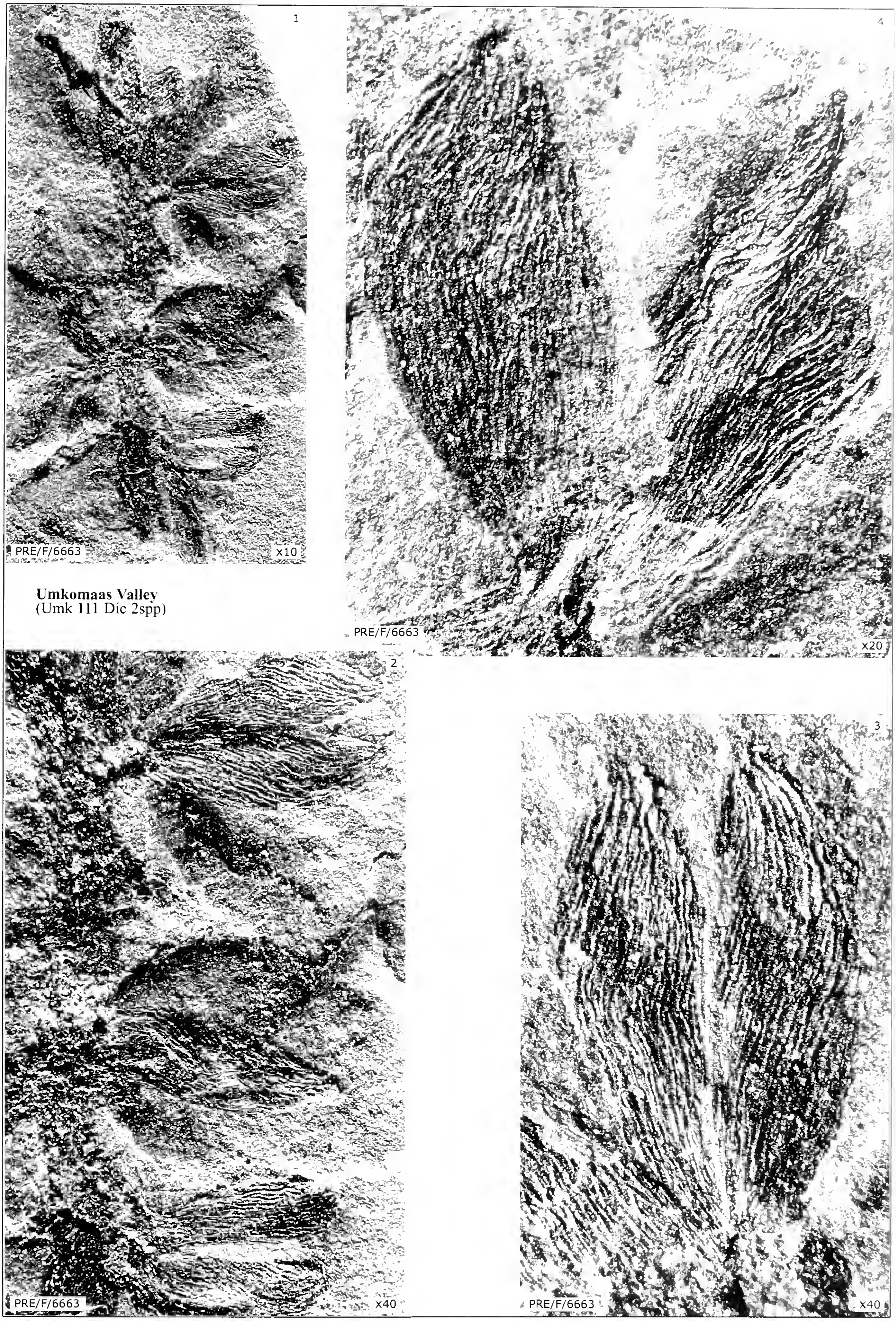
all PRE/F/6773b



Umkomaas Valley
(Umk 111 Dic 2spp)







Umkomaas Valley
(Umk 111 Dic 2spp)

Scytophyllum J.B.Bornemann 1856

Type species
Scytophyllum bergeri J.B.Bornemann 1856.
Mühlhausen, Germany; ?Keuper, Triassic.

Generic concept
A ginkgoopsid leaf with robust blistered rhachis, lanceolate, pinnate-pinnatisect lamina and zwischenfiedern coherent with pinnae.

Generic characters (Molteno Fm.)
Attachment: unknown.
Leaf: pinnate-pinnatisect, lanceolate, medium-sized; petiole unknown; rhachis robust with characteristic blisters; pinnae opposite to subopposite, short, broadly tapering, apex rounded, with coherent pinna-like zwischenfiedern; veins lepidopteroid, midrib tapering, secondary veins fine and give rise to simple or forking tertiary veins which sometimes conjoin.
Cuticles: see text adjacent.

Etymology
Scytophyllum—*skytos* (Gr.), leathery; *phyllom* (Gr.), leaved.

Global range: several spp., Pangaea, L.Tr.–L.J.

Gondwana Triassic occurrence
Frequency (F): 1 degree square (of the 84 across Gondwana).
Ubiquity (U): 1 continent (of 5 comprising Gondwana).
Diversity (D): 1 foliage species.
Abundance (A): <1% (as recorded for the Molteno).
Longevity (L): 1 myrs (Lower Carnian).

Colonisation success: FUDAL rating 1/1/1/–/1 = 4.
Minimum success (Grade 1): *Scytophyllum*, as understood here, was one of the three least prominent genera in the Gondwana Triassic.
Endemism: the Molteno species is a single-assemblage endemic.

Molteno occurrence
Frequency (F): 1 TC (of 100 sampled in the Molteno).
Diversity (D): 1 species.
Abundance (A): 1 indiv., extremely rare.

Habit: possibly a shrub.
Preferred habitat: *Dicroidium* riparian forest.

Affiliated organs: unknown for Molteno.

Classification & comparison
Scytophyllum often forms an integrating series with *Lepidopteris* as pointed out by Dobruskina (1975, p. 536), Holmes (1982, p. 22) and And. & And (1989, pp. 65, 88). The species described here from Umk 111 has the completely coherent form as is diagnostic for *Scytophyllum*.

Vittaephyllum Dobruskina 1975 (U. Permian to U. Triassic of the USSR), from the general appearance of the lamina, is evidently related to *Lepidopteris*, but in its forking frond it is reminiscent of *Dicroidium*.

Krassilov (1991, 1995, 1997) records some interesting ideas on the question of the origin of angiosperm leaves from the coalescing of adjacent veins as in *Scytophyllum* leaves.

Scytophyllum austroafricanum J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/399; pl. 49(1–3).
Assemblage (TC): Umk 111 Dic 2spp, Umkomaas Valley.
Preservation: nearly complete leaf, without counterpart; compression in thinly laminated, carbonaceous (good cuticle), moderately baked, dark grey shale with good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 1 individual.

Sister palaeodemes: nil.

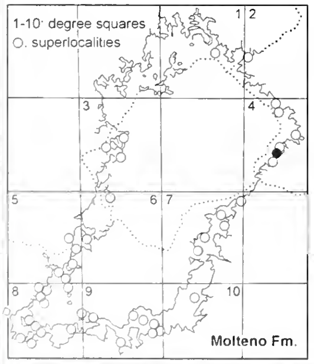
Specific diagnosis
A *Scytophyllum* species with a coherent lamina of pinna lobes and zwischenfiedern.

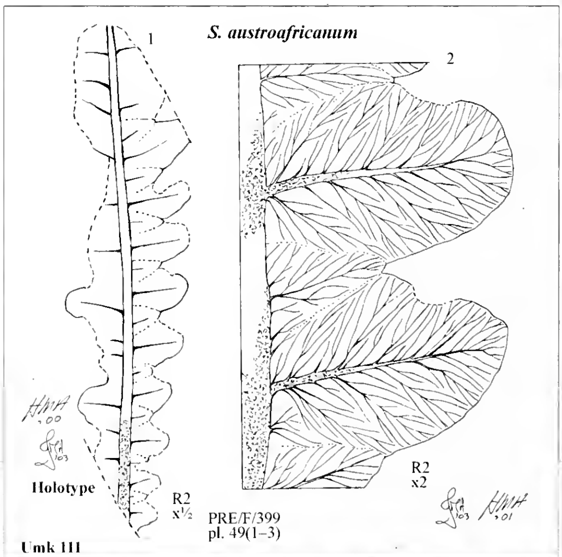
Specific characters
Leaf: length unknown, at least 140 mm long; petiole unknown, rhachis *ca* 3 mm wide; pinna lobes vary from small (7 x 7 mm) at base to larger (20 x 12 mm) in central area, opposite to alternate, entire to sinuate, with characteristic small triangular zwischenfiedern between and coalescing with the larger pinna lobes; venation complex, with tertiary veins that may coalesce when lying in close proximity to each other.

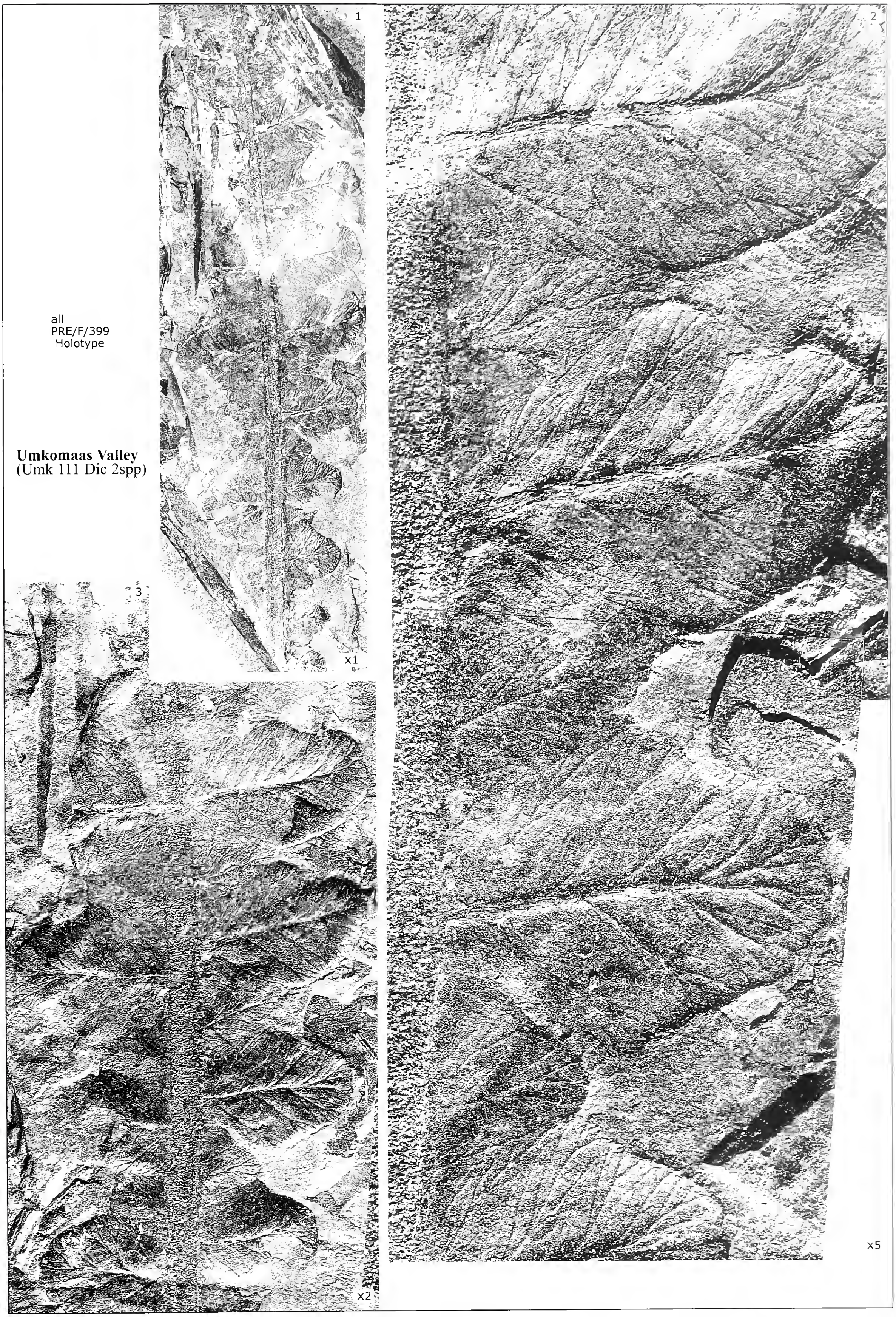
Etymology
austroafricanum—with reference to the South African origin of the species.

Comment & comparison
This single specimen, with coherent pinnae and complex venation, is placed in the genus *Scytophyllum*. It is similar in part to *S. vulgare* from the Late Triassic of the Eastern Urals (Dobruskina 1969; Krassilov 1997), which is polymorphic. The Molteno species is different from partially coherent forms of *Lepidopteris africana* in which the pinnae are usually two to four times longer than wide. The two South American (Argentina) records of *Scytophyllum*, *S. neuburgianum* and *S. bonettiae* (Zamuner & Artabe 1990; Zamuner *et al.* 1999), are here regarded as more likely to belong to the genus *Lepidopteris*.

Cuticles
Potential sample: Umk 111, 1 indiv.
Macerated (this work): 1 indiv.
Preservation grade: Grade 3, tiny pieces.
Diagnostic characters: not available.
Comment: The reason for our preparing cuticle samples was to assess the similarity between this single individual of *S. austroafricanum* and *Lepidopteris* (both included in the Peltaspermaceae) on the one hand, and the foliage genus *Kurtziana* (in the adjacent order) on the other. The tiny fragments of Grade 3 cuticle were insufficient for comparisons.
Significance: of no aid in classification and affiliation.







all
PRE/F/399
Holotype

Umkomaas Valley
(Umk 111 Dic 2spp)

GINKGOOPSIDA S.V.Meyen 1984
MATATIELLALES J.M.And. & H.M.And., ord. nov.
MATATIELLACEAE J.M.And. & H.M.And., fam. nov.

Matatiella J.M.And. & H.M.And., gen. nov.

Type species
Matatiella rosetta J.M.And. & H.M.And., sp. nov.
Matatiele, Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis
A ginkgoopsid strobilus of linear-cylindrical shape with megasporophylls consisting of single, reflexed, variously lobed palmate heads.

Generic characters
Strobilus: simple, racemose, compact, radially symmetrical, of medium size (*ca* 90 mm long); axis relatively stout, erect; megasporophylls numerous, helically arranged.
Megasporophyll: simple, pedunculate; ovuliferous heads palmate (10 x 8 mm), recurved, 4–6-lobed; ovules/seeds (?)adaxial, enclosed by thin protective membrane, 1 per lobe.
Ovule: oval (2 x 1.5 mm), unwinged.

Etymology
Matatiella—after the type locality Matatiele.

Global range: 5 spp., Gondwana, Tr. (LAD–CRN).
First: *Matatiella* sp. indet. (Retallack 1981b); Long Gully Fm., Benmore Dam region, New Zealand.
Last: the 4 Molteno species described here.

Gondwana Triassic occurrence
SAf—Karoo Basin, 4 TCs (17 indivs).
Aus—New Zealand, 3 TCs (24 indivs).

Molteno occurrence
Frequency (F): 4 TCs (of 100 sampled in the Molteno).
Diversity (D): 4 species.
Abundance (A): 17 individuals total, very rare to vanishingly rare.

Pen 411 Hei elo:	7 indivs. in	70 man-hours	(1 per 1 man-day)	very rare
Mat 111 Dic dub:	6 "	" 65 "	(1 " 1 ")	"
Kan 111 Ast spA:	3 "	" 30 "	(1 " 1 ")	"
Aas 411 Dic/Sph:	1 "	" 512 "	(1 " 51 ")	vanish. rare

Matatiella is an infrequent and very rare element in the Molteno. Notably, it is represented by a distinct species in each palaeodeme.

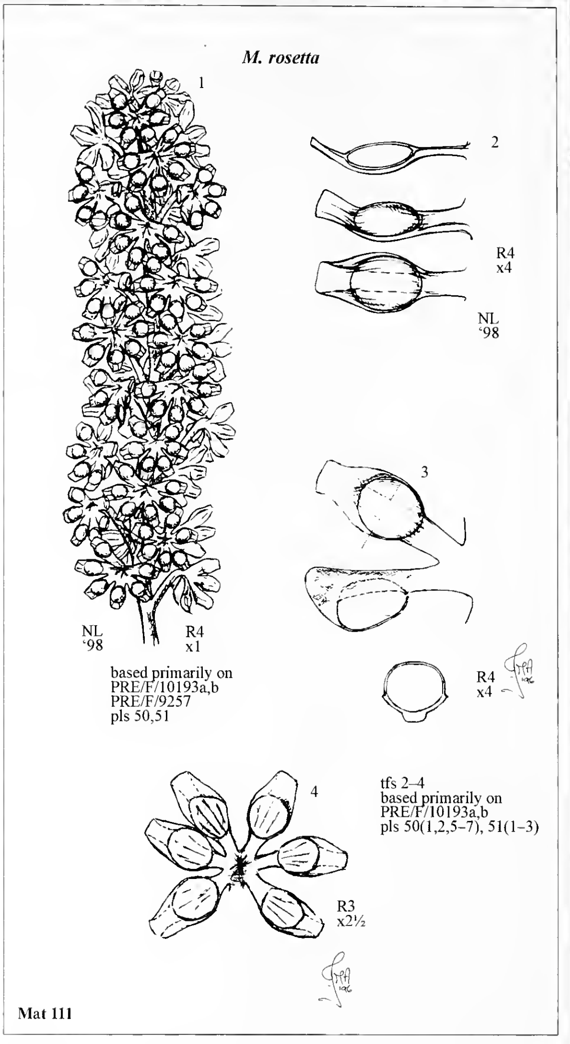
Affiliated organs
Male strobilus: unknown.
Foliage: *Kurtziana*—Grade 2 (Mut. occ.).

Classification & comparison
Suprageneric classification (Matatiellaceae/Matatiellales)

Of all known global Triassic megasporangiate strobili, *Peltaspermum* is the only genus with some overall similarity to *Matatiella*. It might seem reasonable to relate the multilobed, peltate, ovuliferous disc of *Peltaspermum* with the lobed, palmate head of *Matatiella*. However, as the megasporophylls of *Peltaspermum* are radially symmetrical and those of *Matatiella* bilaterally symmetrical, their separation at order level appears to be justified. *Matatiella* is placed in the new family Matatiellaceae and order Matatiellales within the class Ginkgoopsida.

Intergeneric classification (Gondwana Triassic)

Considering the full set of seven Molteno ginkgoopsid megasporangiate genera—*Peltaspermum*, *Matatiella*, *Avatia*, *Hamshawvia*, *Umkomasia*, *Kannaskoppia* and *Cetifructus*—*Peltaspermum*, as noted above, is the only strobilus at all like *Hamshawvia*. When individual megasporophylls are viewed alone, then *Avatia*, with its palmate heads, comes closest. These differ most evidently in bearing readily dehisced winged seeds.



Reconstructions

The full R4 reconstruction is based on the two almost complete Mat 111 *M. rosetta* strobili shown on pls 50, 51. As no clear tip is preserved, the total length of the strobilus is uncertain. An apparent base is preserved in PRE/F/10193b—suggested by the absence of megasporophylls along the axis (which, however, dips into the matrix). Possible tips are preserved in the specimens from Kan 111 and Pen 411, but there are no clear bases.

In most specimens it is difficult to decide whether the ovules are attached on the abaxial or adaxial side of the megasporophyll. The strobilus reconstruction is drawn with the ovules in an adaxial position as that is how they appear to be in the material from the type locality Mat 111. However, at Kannaskop (Kan 111), a strobilus, PRE/F/13503a, is preserved showing a cross section of a megasporophyll head, seemingly attached to the main axis and with ovules apparently in an abaxial position—pl. 52(3); p. 174, tf. 4b.

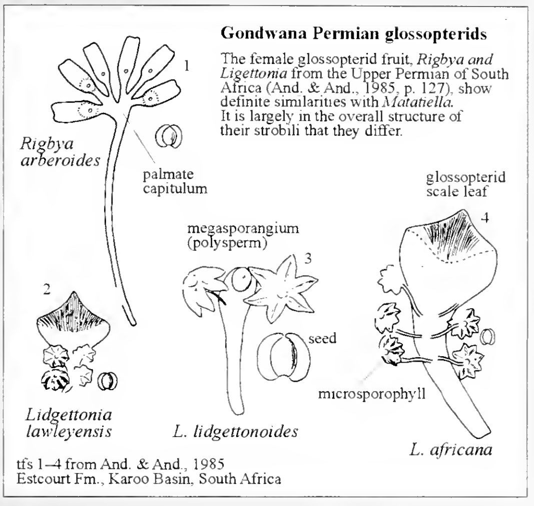
Evidence for affiliation of organs

Mutual occurrence

We have given *Matatiella* a Grade 2 affiliation with *Kurtziana* based on mutual occurrence in four Molteno TCs (Tab. 44). In these four TCs, *Kurtziana* is always below 1% of the total flora although one would expect higher numbers if *Matatiella* was indeed its affiliate. In the two TCs where *Kurtziana* is quite common (Lut 511, 20% and Kon 111, 5%) no *Matatiella* has been found. Our affiliation rating is supported by the New Zealand occurrences.

New Zealand

In New Zealand, *Matatiella cournanei* (formerly *Peltaspermum cournanei*) has been affiliated with *Pachydermophyllum praecordillera* at three TCs (Retallack 1981b, 1983; Pole & Raine 1994). *Pachydermophyllum* is a northern hemisphere genus based on Yorkshire Jurassic fronds. The Gondwana material requires revision. We consider it may be allied to, if not the same as *Kurtziana*.



Adaptive radiation *(Molteno diversity)*

On the basis of the limited collection of *Matatiella* available—a total of 17 individuals—a different species appears to characterise each of the four TCs/reference palaeodemes. The affiliated leaf genus *Kurtziana* shows much greater diversity, with some 16 species occurring. The four species are distinguished by features of the megasporophylls, most notably the number and nature of the ovuliferous lobes.

Each species represents a different habitat with a distinctive assemblage of plants, and derives from a different stratigraphical level.

M. rosetta—Mat 111 Dic dub (Matatiele); 6 indivs
Dicroidium riparian forest (immature); Cycle 2b (Indwe Member)
M. hemirosetta—Kan 111 Dic dub (Kannaskop); 3 indivs
fern/*Kannaskoppia* meadow; Cycle 3 (Mayaputi Member)
M. sessilis—Pen 411 Hei elo (Peninsula); 7 indivs
Heidiphyllum thicket; Cycle 2f (Indwe Member)
M. reducta—Aas 411 Dic/Sph (Aasvoëlberg); 1 indiv.
Sphenobaiera closed woodland; Cycle 1 (Bamboesberg Member)

Gondwana Triassic occurrence (elaborated)

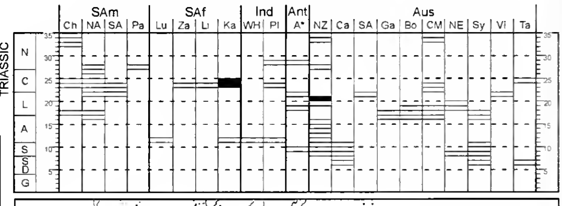
The specimens described by Pole & Raine (1994) from New Zealand as *Peltaspermum cournanei* can now be placed in the new genus *Matatiella* as *M. cournanei* (Pole & Raine) J.M.And. & H.M.And., comb. nov. They show no distal extension to the ovuliferous lobe and are closest to *M. reducta* described below.

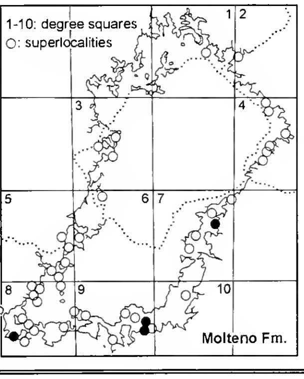
Tab. 43.

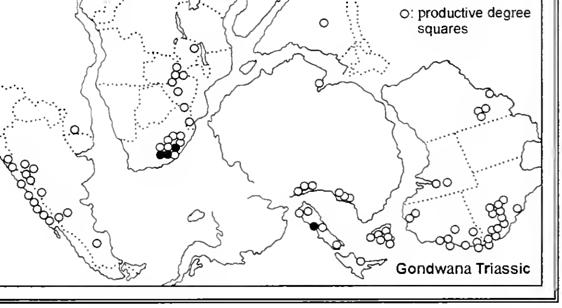
***MATATIELLA* HYPODIGM, Gondwana Triassic occurrence**

AUTHOR		SUBREGION		FORMATION		LOCALITY	NAME	ILLUSTRATION		Species: Molteno *M. ros.*	*M. hem.*	*M. ses.*	*M. red.*	Other *M. cou.*	*sp. indet*
New Zealand															
1981b	Retallack	Benmore dam	NZ4	21	Long Gully Farm	Long Gully	(?) *Peltaspermum* sp.	1	f 3(B)	-	-	-	-	-	1
1983	"	" "	"	"	Bl. Jacks Congl.	nr. Benmore Dam	*Peltaspermum*	3	f 6(F-H), f 10(G-I)	-	-	-	-	3?	-
1994	Pole & Raine	Invercargill	?	?	?	Pollack Road *	*Antevsia*	1	f 5(A), 6(D)	-	-	-	-	1?	-
"	"	"	"	"	"	" "	*P. cournanei*	20	f 5(B-G), 7(A-G)	-	-	-	-	20	-
* all from same horizon, F46/F067															

GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION







Matatiella rosetta J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/10193a,b; pls 50(1, 2, 5–7), 51(1–3).
Assemblage (TC): Mat 111 Dic dub, Matatiele.
Preservation: central portion of cone, part and counterpart; impression, in thickly laminated, olive-grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 6 indivs (2 intact, 3 partial, 1 isolated), pls 50(1–7), 51(1–5).

Sister palaeodemes—nil.

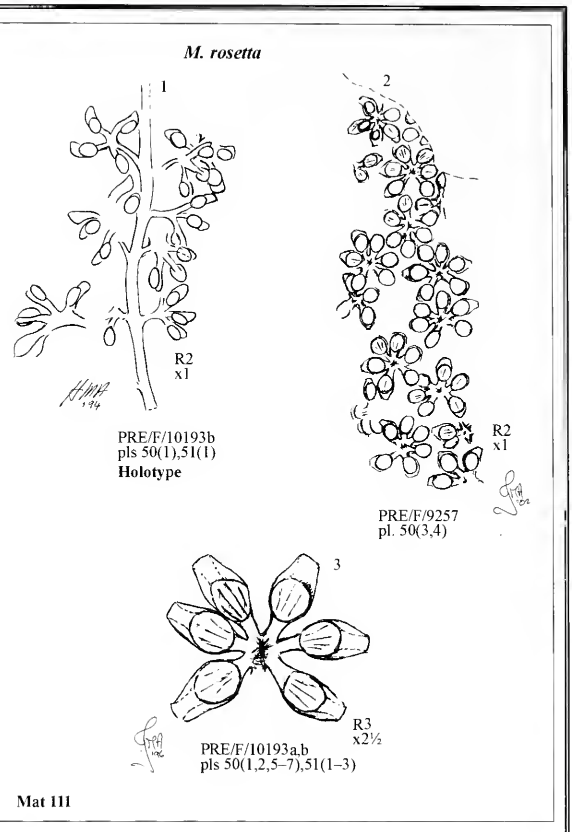
Specific diagnosis
A *Matatiella* species bearing megasporophylls with 6 deeply divided ovuliferous lobes forming a full rosette.

Specific characters
Megasporophyll: ovuliferous heads 6-lobed, forming a full rosette; lobes deeply divided, distinctly narrowed towards base, extending well distal of the ovule and tapering to a truncate apex.

Etymology
rosetta—referring to the rosette form of the megasporophyll.

Comments & comparison
M. rosetta differs from other *Matatiella* species in the lobes which are deeply divided to well beyond the ovules and almost to the centre of the megasporophyll.

The high proportion of articulated and reasonably intact specimens of this and other fruit taxa from Matatiele (Mat 111) suggests that it was an autochthonous to near-autochthonous deposit.



Matatiella hemirosetta J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/13503a,b; pl. 52(1, 3, 7).
Assemblage (TC): Kan 111 Ast spA, Kannaskop.
Preservation: central portion of cone, part and counterpart; impression, in thick-bedded, moderately baked, greenish grey, silty mudstone with very poor cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 3 indivs (1 intact, 2 partial), pl. 52(1–7).

Sister palaeodemes—nil.

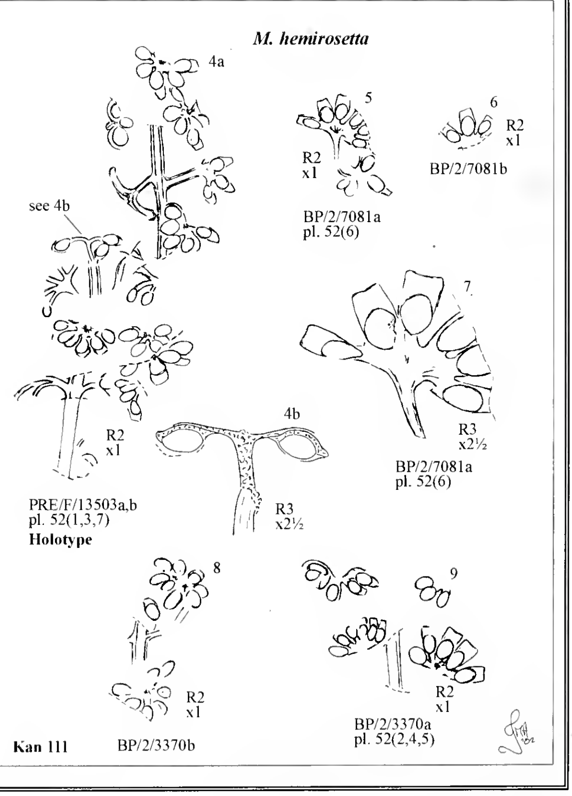
Specific diagnosis
A *Matatiella* species bearing megasporophylls with 6 moderately divided ovuliferous lobes forming a half rosette.

Specific characters
Megasporophyll: ovuliferous heads 6-lobed, forming a half rosette; lobes moderately divided, extending well distal of the ovule to a broad truncate apex.

Etymology
hemirosetta—referring to the half-rosette form of the megasporophyll.

Comments & comparison
M. hemirosetta differs from other *Matatiella* species in the semicircular shape and less deeply divided lobes of the megasporophyll.

The three articulated individuals of *M. hemirosetta* and the uniquely intact preservation of other fruit and foliage taxa from Kannaskop (Kan 111) suggest that this too (see text for *M. rosetta*) was an autochthonous deposit.



Matatiella sessilis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/17942a,b; pl. 53(5–7).
Assemblage (TC): Pen 411 Hei elo, Peninsula.
Preservation: a single megasporophyll head, part and counterpart; impression, in thickly laminated, greenish grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 7 indivs (1 intact, 3 partial, 3 isolated), pl. 53(1–9).

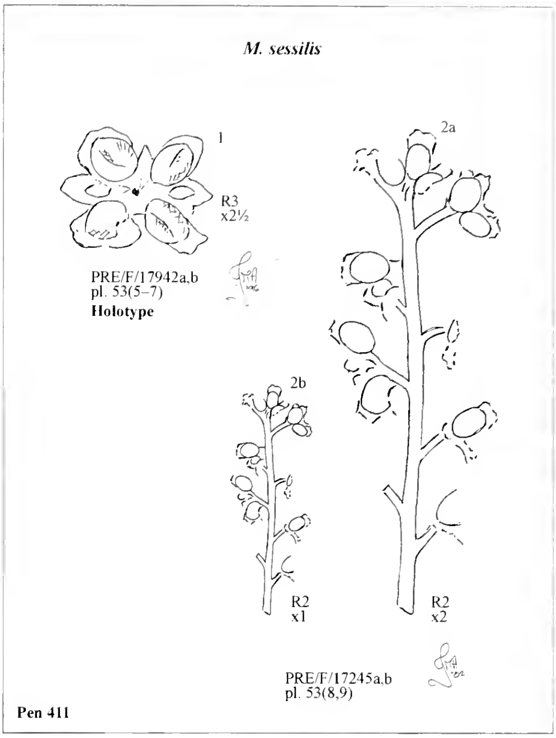
Sister palaeodemes—nil.

Specific diagnosis
A *Matatiella* species bearing megasporophylls with 6 or 4 (2 aborted), shallowly divided ovuliferous lobes.

Specific characters
Megasporophyll: ovuliferous heads 6- or 4-lobed (sometimes with 2 ovules aborted), forming a full rosette; lobes shallowly divided, extending slightly beyond the ovule to irregularly rounded apex.

Etymology
sessilis—referring to the sessile megasporophyll lobes.

Comments & comparison
M. sessilis differs from other *Matatiella* species in the very shallowly divided megasporophyll lobes which barely extend beyond the ovule. A further characteristic, apparently unique to this species and none too certain in view of the limited sample, is the tendency for some of the ovules to abort (tf. 1 adjacent).



Matatiella reducta J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/20536; pl. 53(10, 11).
Assemblage (TC): Aas 411 Dic/Sph, Aasvoëlberg.
Preservation: a single megasporophyll head, without counterpart; impression, in thinly laminated, strongly baked, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 1 indiv. (isolated), pl. 53(10, 11).

Sister palaeodemes—nil.

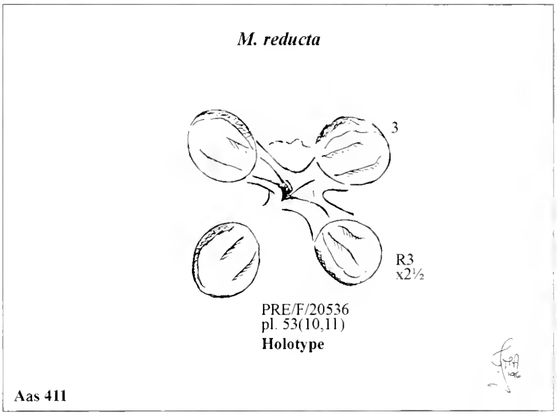
Specific diagnosis
A *Matatiella* species bearing megasporophylls with 4 deeply divided ovuliferous lobes not extending beyond the ovule.

Specific characters
Megasporophyll: ovuliferous heads 4-lobed, forming a full rosette; lobes deeply divided, not extending beyond ovules.

Etymology
reducta—referring to the reduced megasporophyll lobes.

Comments & comparison
This species, based on a single specimen, is not as secure as the previous three described from the Molteno. It differs from those species in having four megasporophyll lobes which do not extend beyond the ovules.

M. reducta is partly reminiscent of *M. cournanei*, originally described as a *Peltaspermum* by Pole & Raine (1994) from New Zealand. That species differs in having six ovulate lobes and is alike in that these show no distal extensions beyond the ovules.



Kurtziana Freng. 1942

Type species
Kurtziana cacheutensis Freng. 1942.
Cacheuta, Argentina; Carnian, Triassic.

Generic concept
A ginkgoopsid leaf with elliptical pinnate lamina and pinnules markedly contracted above and decurrent below.

Generic characters (Molteno Fm.)
Attachment: unknown.
Leaf: pinnate, elliptical, medium-sized; petiole distinct, of moderate length; pinnae generally closely spaced, opposite to subopposite, ovate to broadly linear, entire, apex obtuse; base contracted above and variously decurrent below; veins simple to twice forked, midrib distinct to apex.
Cuticle: see text adjacent.

Eponymy
Kurtziana—for F. Kurtz, an eminent South American palaeobotanist.

Global range: *ca* 20 spp., Gondwana, Tr.–J. (LAD–HET).
First: *Kurtziana* sp. (Walkom 1928); Esk Beds, Wivenhoe, Australia.
Last: *Kurtziana brandmayri* (Artabe *et al.* 1991); Nestares Fm., Alicurá, Neuquén Province, Argentina.

Gondwana Triassic occurrence (after And. & And. 1989)
Frequency (F): 6 degree squares (of the 84 across Gondwana).
Ubiquity (U): 2 continents (of 5 comprising Gondwana).
Diversity (D): *ca* 20 foliage species.
Abundance (A): <1% (the norm in Molteno TCs).
Longevity (L): 2 myrs (Lower Ladinian to Liassic).

Colonisation success: FUDAL rating 6/2/20/–/2 = 30.
Intermediate success (Grade 3): *Kurtziana* was the 12th most prominent genus in the Gondwana Triassic; it was diverse, but of moderate frequency and abundance.
Endemism: the 20 species are mainly single-assemblage endemics.

Molteno occurrence
Frequency (F): 13 TCs (of 100 sampled in the Molteno).
Diversity (D): 16 species.
Abundance (A): co-dominant (20%) in 1 TC; common (5%) in 1 TC; rare to very rare (<1%) in other 11 TCs.

Habit: possibly a small spreading tree.
Preferred habitat: on the periphery of *Heidiphyllum* thicket.

Affiliated organs
Female strobilus: *Matatiella*, Grade 2 (Mut. occ.).
Male strobilus: not known.

Classification & comparison
Intergeneric comparison
In frond morphology and venation pattern, *Kurtziana* differs from all other Gondwana ginkgoopsid leaf genera. Certain northern hemisphere genera have previously been used for Gondwana leaves, some of which, e.g. *Pachypteris* and *Pachydermophyllum*, may be better placed in *Kurtziana*.

Kurtziana was placed in the Cycadales by Artabe & Stevenson (1999). This was based on *K. brandmayri* (leaf and cuticle) from the Jurassic of Neuquén Province, Argentina, as described by Artabe *et al.* (1991). However, we feel there is no clear case for cycadalean affiliation based only on cuticle which does not show clearly preserved stomata and subsidiary cells.

In view of the possible affiliation (Grade 2) with *Matatiella* megasporophylls, we place *Kurtziana* in the Ginkgoopsida.

Interspecific comparison
Kurtziana has not been studied systematically on a Gondwana-wide basis and the specimens included here may not all belong to the same natural genus. Cuticular studies should prove useful in indicating whether *Kurtziana*, as conceived here, is indeed a natural genus or a form-genus with many unrelated species. While we have included the type species, *K. cacheutensis*, in the distribution map, the following two possible records from Australia have not been plotted:

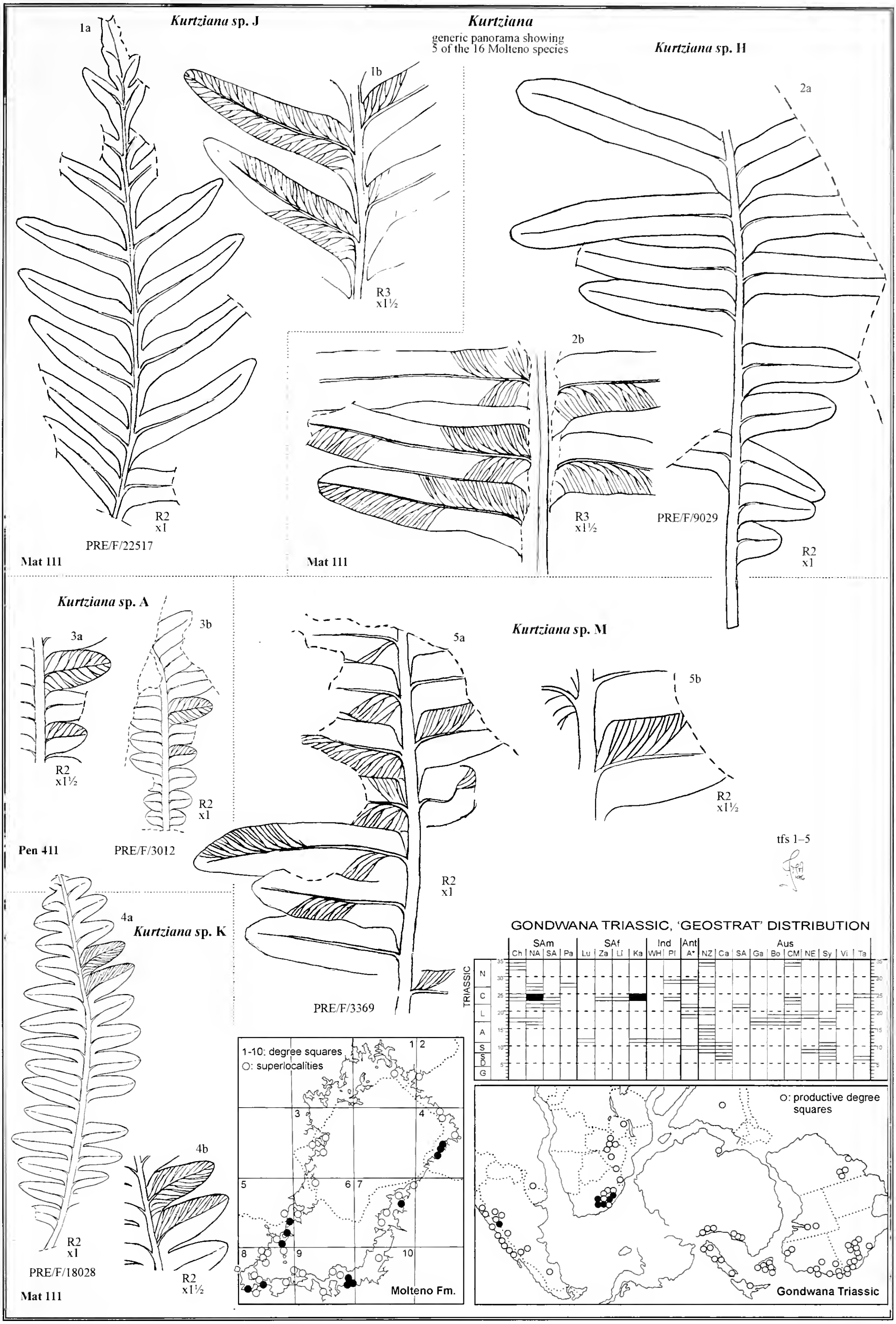
Thinnfeldia eskensis [Walkom 1928, pl. 28(1)]; Esk beds, Wivenhoe, Queensland.
Dicroidium eskense [Flint & Gould 1975, pl. 2(3)]; Basin Creek Fm., Nymboida, N.S.W.

From our Molteno collections we have provisionally recognised 16 *Kurtziana* species (Tab. 44). They remain undescribed and unnamed. Five are illustrated opposite.

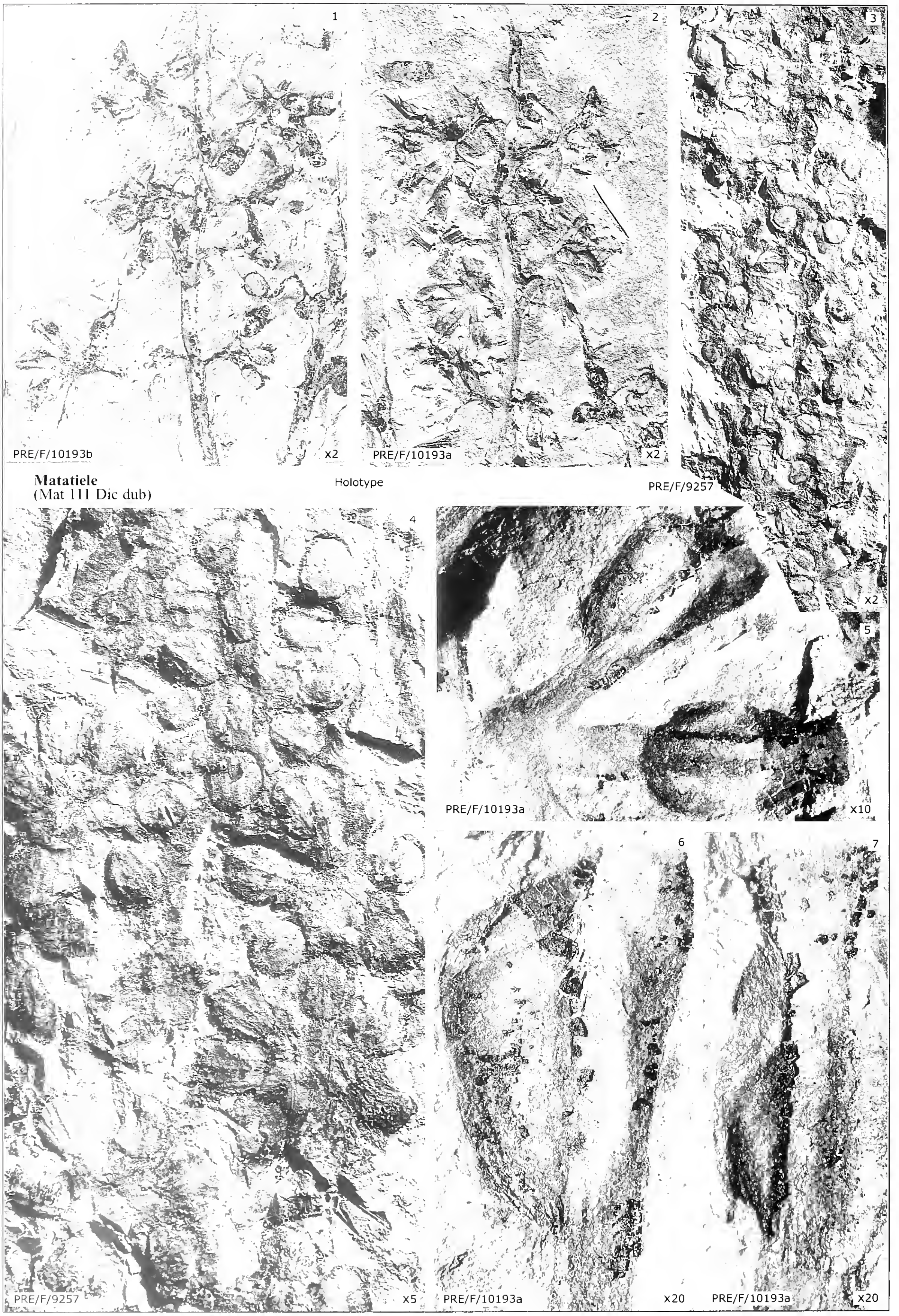
Cuticles
Potential sample: Umk 111, 18 indivs.
Macerated (this work): 6 indivs.
Preservation grade: Grade 3.
Diagnostic characters: marginally present.
Comment: some cellular structure available from 5 indivs, but not yet studied.
Significance: of no obvious aid in classification or affiliation.

assemblages (taphocoenosis)		*Kurtziana*	Species																♀ *Matatiella*	Species				Intactness		
			K. sp A (Mat 111)	" sp B (Boe 112)	" sp C (Boe 112)	" sp D (Kon 111)	" sp E (Vin 111)	" sp F (Umk 111)	" *cach.* (Umk 111)	" sp G (Hla 213)	" sp H (Mat 111)	" sp I (Umk 111)	" sp J (Mat 111)	" sp K (Pen 411)	" sp L (Lut 511)	" sp M (Kan 111)	" sp N (Lut 311)	" sp O (Umk 111)		*M. rosetta*	*M. hemirosetta*	*M. sessilis*	*M. reducta*	Intact strobili	Fragm. strobili	Isolated heads
Boe 112	Dic cor	3	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kan 111	Ast spA	2	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	3	-	3	-	-	1	2	-
Vin 111	Dic odo	7	-	-	-	-	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kra 111	" "	4	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lut 511	Hei elo	**20**	-	-	-	-	-	-	-	-	-	-	-	-	**20**	-	-	-	-	-	-	-	-	-	-	-
" 311	" "	5	-	-	-	-	4	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Kon 111	" "	**5**	-	-	-	**5**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pen 411	Hei elo	50	-	-	-	-	-	-	-	-	-	-	-	50	-	-	-	-	7	-	-	7	-	-	4	3
Hla 213	Dic elo	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Umk 111	Dic 2spp	18	-	-	-	2	-	1	2	-	-	4	2	-	-	-	-	6	-	-	-	-	-	-	-	-
San 111	Dic cra	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mat 111	Dic dub	3	2	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	6	6	-	-	-	2	3	1
Aas 411	Dic/Sph	15	-	-	-	-	-	-	-	-	-	-	-	15	-	-	-	-	1	-	-	-	1	-	-	1
Totals TCs		13	1	1	1	2	2	1	3	1	1	1	2	2	1	1	1	1	4	1	1	1	1	2	3	3
Total indivs		%	2	2	1	%	11	1	7	1	1	4	3	65	%	2	1	6	17	6	3	7	1	3	9	5

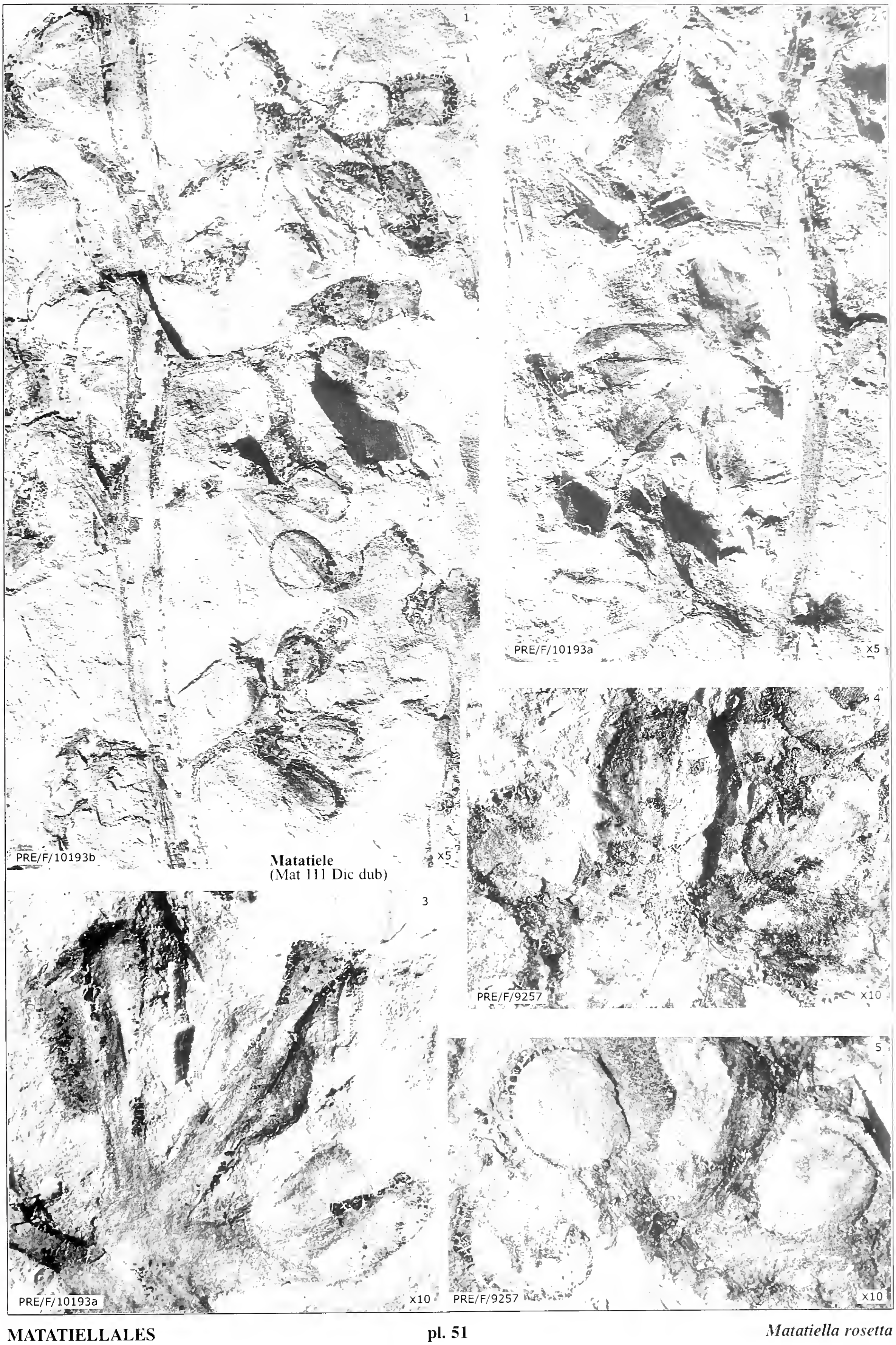
Tab. 44. ***Matatiella/Kurtziana*, Molteno occurrence**



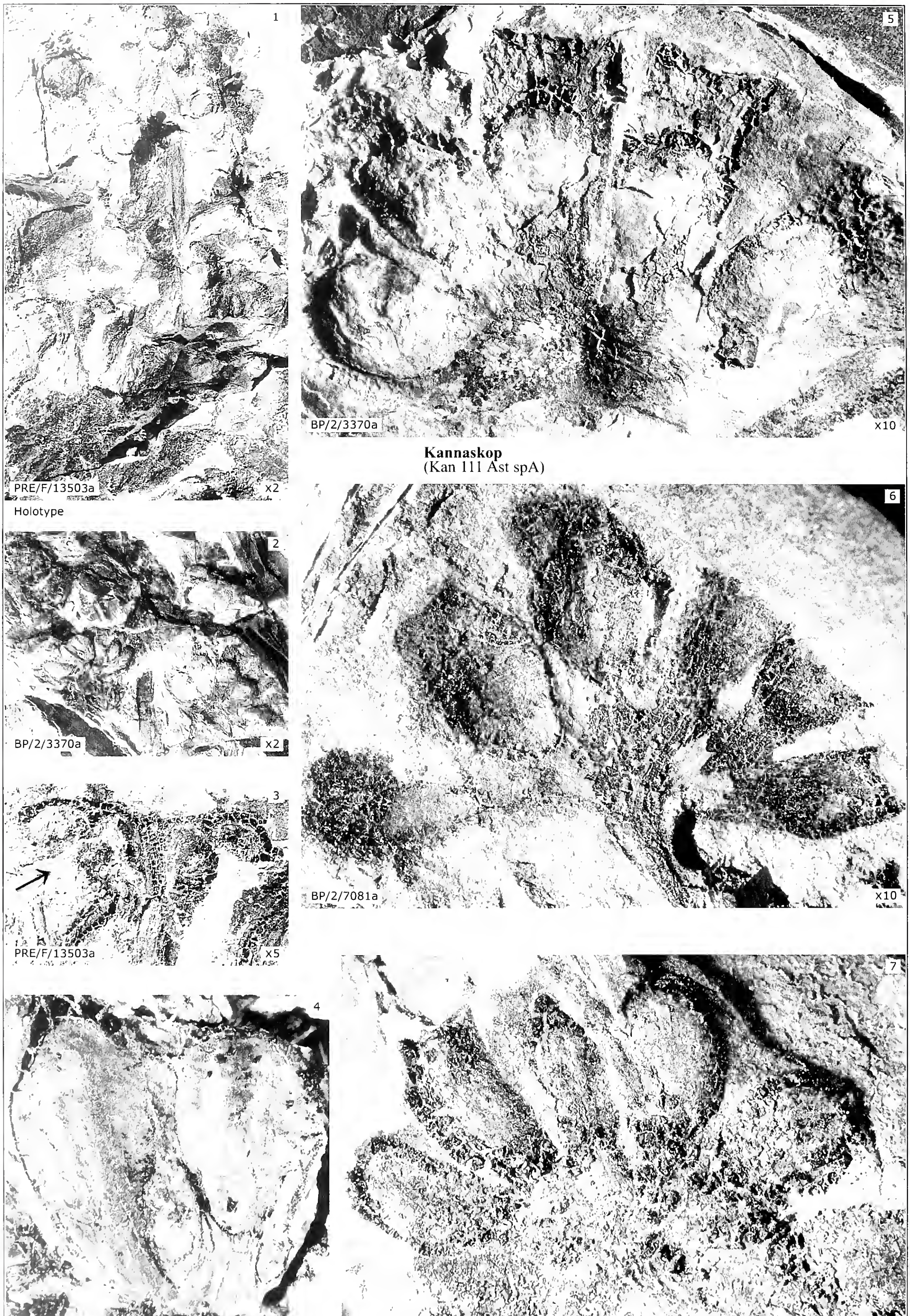
Kurtziana
generic panorama showing
5 of the 16 Molteno species
Kurtziana sp. J
1a
1b
R3
x1½
R2
x1
PRE/F/22517
Mat 111
Kurtziana sp. H
2a
2b
R3
x1½
PRE/F/9029
R2
x1
Mat 111
Kurtziana sp. A
3a
3b
R2
x1½
R2
x1
Pen 411
PRE/F/3012
Kurtziana sp. M
5a
5b
R2
x1½
R2
x1
PRE/F/3369
tfs 1–5
4a
Kurtziana sp. K
4b
R2
x1
PRE/F/18028
R2
x1½
Mat 111
GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION
SAm
Ch NA SA Pa
SAf
Lu Za Li Ka
Ind
WH Pl
Ant
A*
Aus
NZ Ca SA Ga Bo CM NE Sy Vi Ta
TRIASSIC
N
C
L
A
S
S
G
1-10: degree squares
○: superlocalities
Molteno Fm.
○: productive degree squares
Gondwana Triassic



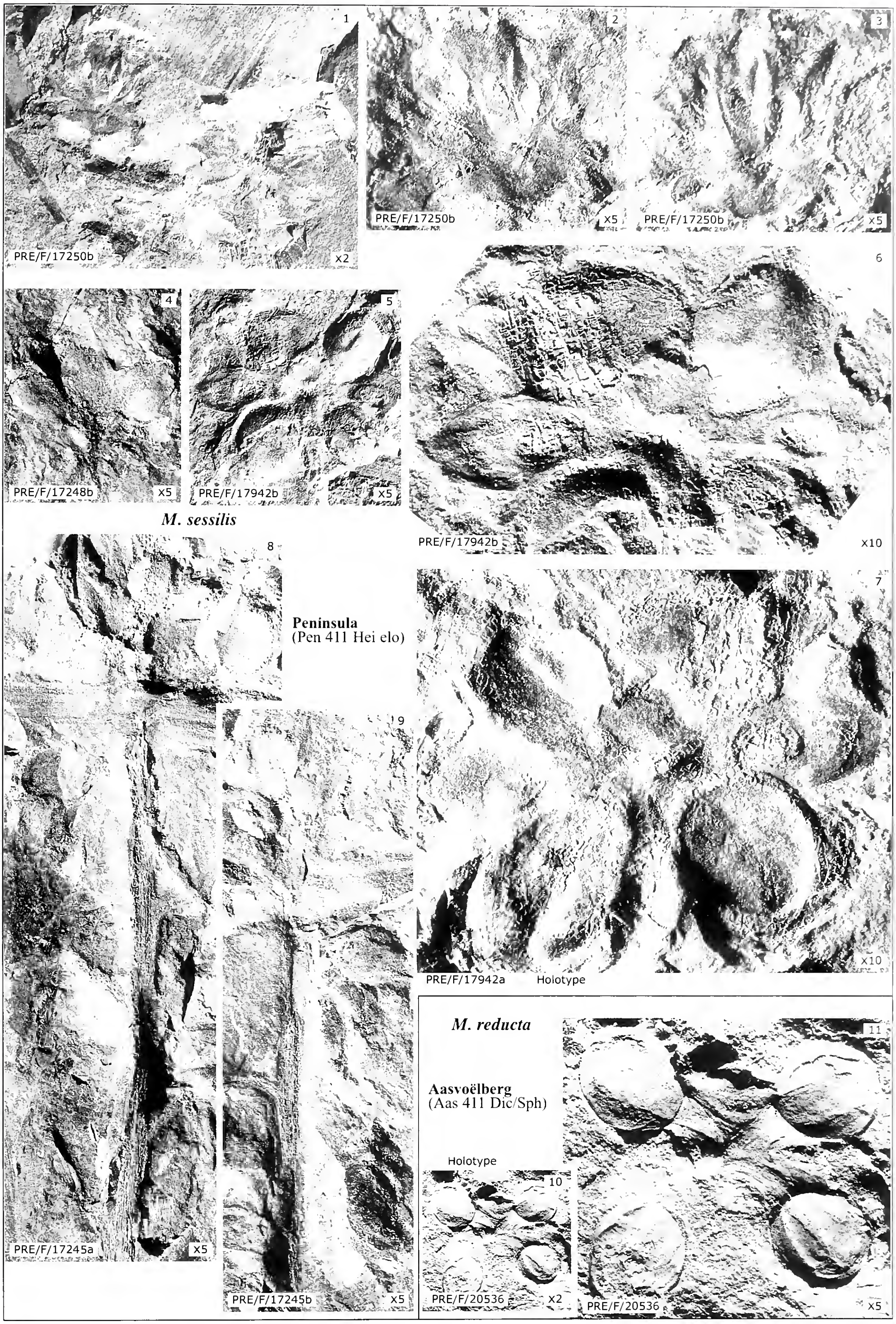
Matatiella rosetta pl. 50 **MATATIELLALES**



MATATIELLALES **pl. 51** *Matatiella rosetta*



Matatiella hemirosetta **pl. 52** **MATATIELLALES**


1
PRE/F/17250b x2
2
PRE/F/17250b x5
3
PRE/F/17250b x5
4
PRE/F/17248b x5
5
PRE/F/17942b x5
6
PRE/F/17942b x10
M. sessilis
8
Peninsula
(Pen 411 Hei elo)
7
PRE/F/17942a Holotype x10
9
PRE/F/17245a x5
PRE/F/17245b x5
M. reducta
Aasvoëlberg
(Aas 411 Dic/Sph)
Holotype
10
PRE/F/20536 x2
11
PRE/F/20536 x5

GINKGOOPSIDA S.V.Meyen 1987
MATATIELLALES J.M.And. & H.M.And., ord. nov.
INCERTAE SEDIS family

Switzianthus J.M.And. & H.M.And., gen. nov.

Type species
Switzianthus moriformis J.M.And. & H.M.And., sp. nov.
Little Switzerland, Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis
A ginkgoopsid male strobilus of compact conate form, with helically arranged microsporophyll scales bearing numerous minute microsporangia with disaccate pollen grains.

Generic characters (based on *S. moriformis*)
Strobilus: a simple compact cone, small to medium (*ca* 25–40 mm long); axis stout, gently curved, free end 3–6 mm; microsporophylls numerous, helically arranged.
Microsporophyll: a simple scale; distal lamina broadly triangular, margin entire, outer rim with fine radiating striae; microsporangia apparently adaxial, numerous, closely packed.
Microsporangium: minute (0.05–0.15 mm diam.), shape uncertain.
Pollen: disaccate.

Etymology
Switzianthus—after the type locality, Little Switzerland.

Global range: 2 spp., Gondwana, Tr. (CRN).
First & last: the 2 Molteno species described here.

Gondwana Triassic occurrence
SAf—Karoo Basin, 3TCs (54 indivs).
Aus—Clarence-Moreton Basin, 1 TC (?indivs).

Molteno occurrence
Frequency (F): 4 TCs (of 100 sampled in the Molteno).
Diversity (D): 2 species.
Abundance (A): 54 individuals total, very rare to extremely rare.

Lit 111 Dic/Hei:	50	indivs	in 550	man-hrs	cleaving	(1	per	1	man-day)	very rare
Win 111 Hei elo:	1	"	" 20	"	"	(1	"	2	")	"
Mat 111 Dic dub:	1	"	" 65	"	"	(1	"	6	")	extr. rare
Aas 411 Dic/Sph:	2	"	" 512	"	"	(1	"	25	")	"

Note that the figures for Lit 111 refer only to curated individuals, a selection of the best seen at the site. The rate of yield of *Switzianthus* at this site may, in reality, be as high as 10 per 1 man-day.

Affiliated organs
Female strobilus: see discussion below.
Foliage: *Dejerseya*—Grade 3 (Cut. corr., Mut. occ.).

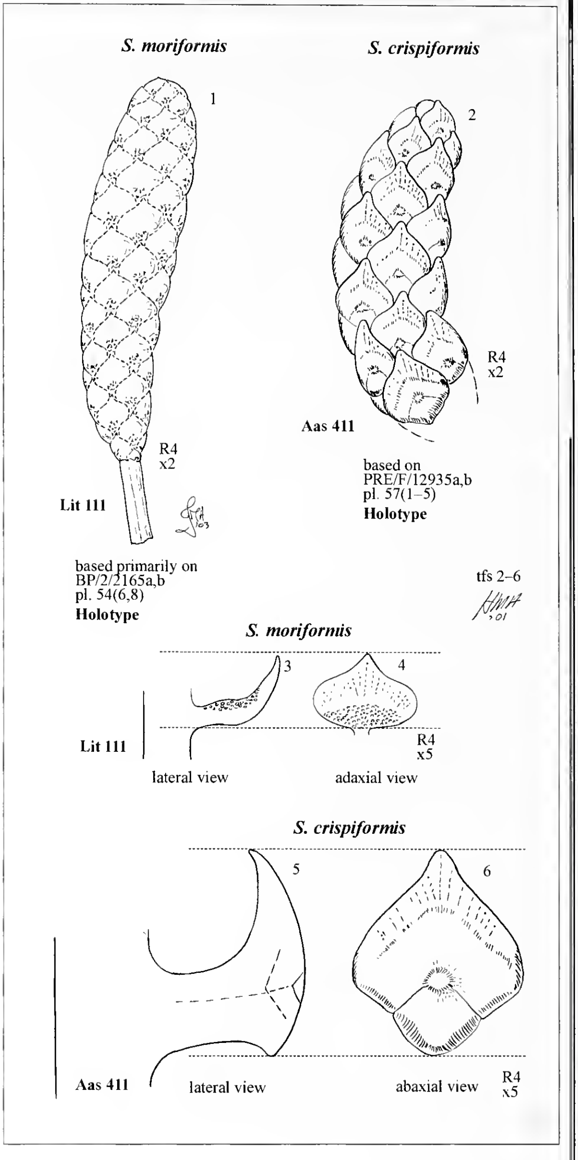
Classification & comparison
Suprageneric classification (fam. Incertae/Matatiellales)

The putative affiliates, *Switzianthus* and *Dejerseya*, present conflicting evidence with regard to their classification. *Switzianthus* is very like *Androstrobus*, which is cycadalean, while *Dejerseya*, in leaf shape, venation and cuticular features, is typically ginkgoopsid. However, the cone scales of *Switzianthus* have a cuticular structure typical of *Dejerseya* and unlike any cycads known to us. Furthermore, the affiliated female structure (known from Dinmore, Australia, see box opposite) also points to a ginkgoopsid connection, in having similarities with *Matatiella*.

Considering the comparison with the ovulate organ *Matatiella*, and since *Dejerseya*, in its pinnate form, comes close to certain species of *Kurtziana* (see p. 177), supposed affiliate of *Matatiella*, we place *Switzianthus* in the order Matatiellales. The sum of differences between the plant-genera *Dejerseya*/*Switzianthus* and *Matatiella*/*Kurtziana* are sufficiently great, however, to suggest that they should belong in distinct families. We leave the family for *Switzianthus* unnamed.

Intergeneric comparison (Gondwana Triassic)

Switzianthus is close to *Androstrobus* in being cone-like and in bearing numerous helically arranged microsporangiate scales. However, typical *Androstrobus* scales (p. 136) are heeled, woody and bear abaxial microsporangia with monosulcate grains, while *S. moriformis* scales are unheeled, apparently fleshy, and bear microsporangia (that are seemingly adaxial) with disaccate pollen grains.



Reconstructions
S. moriformis (Lit 111): Only a few cones in the 50-specimen *S. moriformis* reference palaeodeme (Lit 111) show a few relatively clear scales, the upper part with striations and the lower with irregularly circular depressions representing microsporangia or at least their attachment sites [pl. 55(1–6)]. The evidence suggests that the microsporangia are adaxial and that most scales, being outer views, show no details of the pollen sacs. Based on the depressions, the microsporangia are very small, 0.05–0.15 mm in diameter at their base. Their shape and length are unknown. Pollen has been isolated but no sporangial sacs were observed. On specimen BP/2/2154 (not illustrated), a central depression indicates the axis of the cone.

S. crispiformis (Aas 411): At Aas 411, the preservation is in 3D and no carbonaceous material is preserved. Circular depressions are visible on some of the scales [pl. 57(5)]. The scale peduncle has not been observed in either of the two available specimens. In the holotype, PRE/F/12935a,b, no axis is preserved and its diameter has been estimated from the overall width of the cone.

Evidence for affiliation of organs

Mutual occurrence

Although *Switzianthus* is found in only two of the five TCs yielding *Dejerseya* (Tab. 45), there is a strong case for affiliation at one of these, namely Lit 111. In that TC, *Dejerseya* (at 20%) is a co-dominant member of the diverse assemblage, and *Switzianthus* is the most common of the seven male-fruit genera identified (Tab. 27). At Win 111, where a single specimen of *Switzianthus* occurs, *Dejerseya* (at 10%) is a particularly common element of the assemblage. At Aas 411, two specimens of *Switzianthus* are present but no *Dejerseya* has been recognised. However, the 15 specimens identified as *Kurtziana* sp. K could conceivably be a species of a deeply pinnate form of *Dejerseya* (see Tab. 44).

Cuticular correspondence

Based on material from Lit 111, the cuticles of *Switzianthus* and the leaf genus *Dejerseya* are so closely similar that it is most likely that the two organs derive from the same natural taxon (see pp. 184, 186).

The Androstrobus *puzzle*

The male cone *Androstrobus* has been affiliated with cycad fronds by Harris (1964). In gross morphology, *Androstrobus* is very similar to *Switzianthus*. Thus, in those Molteno TCs where cuticle is not preserved, it is unsure whether we are dealing with *Androstrobus* or *Switzianthus*. We have described two specimens from Aas 411 as *Switzianthus* even though the presence at that TC of cycad leaves (*Pseudoctenis*, Tab. 45) suggests the possibility that they may belong in *Androstrobus*.

Comparisons beyond the Molteno

Australia

Dejerseya is known from several localities in Queensland and Tasmania. One of us (HMA) visited the Dinmore locality at Ipswich, Queensland, in 1988 and observed numerous large slabs with bedding-plane assemblages consisting exclusively of simple to pinnate *Dejerseya* leaves and accompanying fertile material. What we regarded at that time as the female strobilus (And. & And. 1989, p. 258) is now identified as *Switzianthus*. In size and shape, the Dinmore microsporophylls (tf. 1 below) are close to *Switzianthus* from Lit 111. The differences in clarity of scale outline possibly lie in the type of preservation, being carbonaceous compressions without well-demarcated scales at Lit 111 and impressions with clear scales at Dinmore.

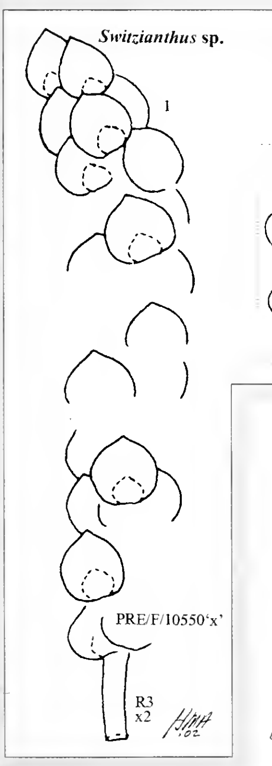
On the same bedding planes at Dinmore there are numerous four-lobed structures (tf. 2 below) of a form not known from the Molteno. These are probably the detached female megasporophylls of *Dejerseya* and show some resemblance to *Fanerotheca* and *Matatiella*.

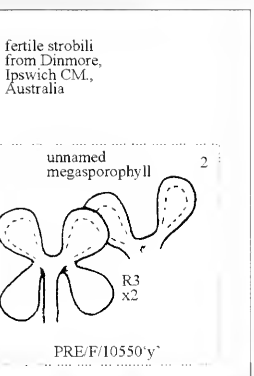
	assemblages (taphocoenoses)		*Dejerseya*	*Pseudoctenis*	*Jeanjacquesia*	*Ctenis*	*Moltenia*	♂ *Switzianthus*	♂ *Androstrobus*
1	Bir 111	Sph 2spp	-	1	1	-	-	-	-
2	Gre 121	Hei elo	**2**	-	-	-	-	-	-
3	Boe 111	Dic/Hei	-	7	-	-	-	-	-
4	Vin 111	Dic odo	-	3	-	-	-	-	-
5	Ela 111	Dic odo	-	2	-	-	-	-	-
6	Kra 311	Dic odo	-	-	-	-	-	-	1
7	Wal 111	Dic odo	-	2	1	-	-	-	-
8	Kon 222	Dic odo	-	**3**	-	-	-	-	-
9	Kon 221	Ast 2spp	-	**25**	-	2	-	-	-
10	Kon 211	"	-	**21**	-	-	-	-	-
11	Kon 111	Dic odo	-	**5**	-	-	-	-	-
12	Pen 321	Dic/Ris	-	1	-	-	-	-	1
13	Pen 221	Dic/Equ	-	2	-	-	-	-	-
14	Pen 431	"	-	**5**	-	-	-	-	-
15	Kap 111	Dic/Ris	-	40	-	-	-	-	-
16	Win 111	Hei elo	**10**	-	-	-	-	1	-
17	Hla 211	Dic 3spp	-	3	-	-	2	-	-
18	" 212	"	-	**1**	-	-	4	-	-
19	" 213	Dic elo	-	27	-	-	7	-	-
20	Umk 111	Dic 2spp	-	**1**	-	1	41	-	-
21	San 111	Dic cra	-	1	-	-	-	-	-
22	Mat 111	Dic dub	-	12	-	-	-	1	-
23	Lit 111	Dic/Hei	**20**	48	6	-	1	50	-
24	Aas 611	Hei elo	**20**	-	-	-	-	-	-
25	" 211	Hei elo	14	-	-	-	-	-	-
26	" 411	Dic sph	-	19	-	-	-	2	-
	Total TCs		5	21	3	2	5	4	2
	Total indivs		%	%	8	3	55	54	2

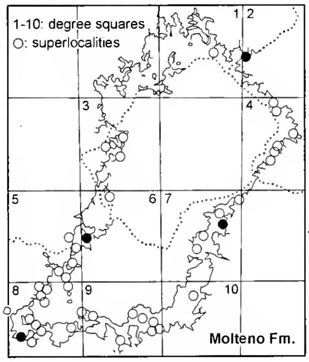
Tab. 45. ***Switzianthus/Dejerseya*, Molteno occurrence**

Comparisons beyond Gondwana Triassic

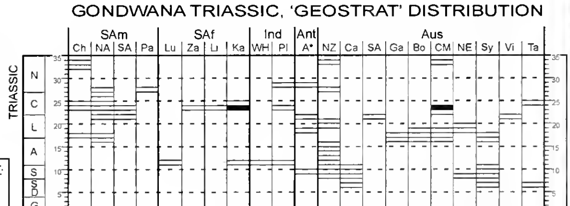
Laurasia Triassic—Switzianthus has some similarity to the male cone of *Bernettia phialophora* from the Rhaeto-Liassic of Greenland, which Harris (1935) attributed to *Sphenobaiera spectabilis* on the basis of repeated co-occurrence and cuticular structure. Interestingly, Harris (1935) noted that *Bernettia* looked very like a cycad male cone, but reasoned that the Ginkgoales could include a wide range of reproductive organs. *Bernettia* differs from *Switzianthus* in yielding nondisaccate grains. *Bernettia phialophora* was transferred to *Androstrobus phialophora* by Van Konijnenburg-Van Cittert (1993).

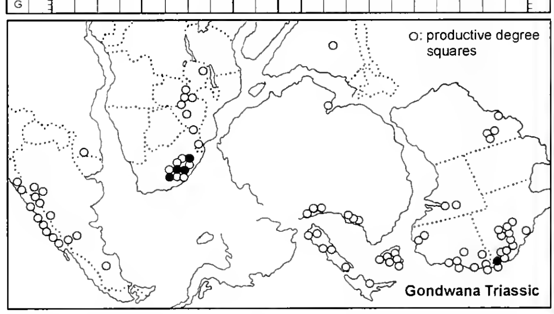






GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION





Cuticles

Potential sample: Lit 111, 50 indivs.

Macerated (this work): 3 indivs.

Preservation grade: Grade 5 (excellent), all features clear, large pieces.

Diagnostic characters: cells isodiametric, walls gently curved, nonpapillate; stomata hypostomatic, nonaligned; subsidiary cells irregular (brachypary)actinocytic, strongly cutinised, walls thickened, florin ring nonlappetate, guard cells probably elliptic.

Comment: both upper and lower cuticle are clearly present, but it cannot be determined which is which.

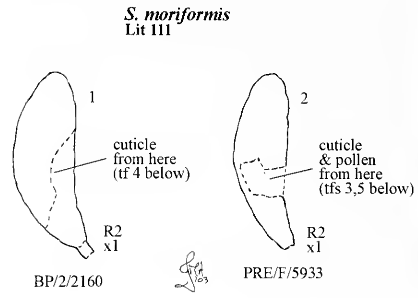
Significance:

Classification—the cuticles, in being so similar to *Dejerseya*, point to *Switzianthus* belonging to the Ginkgoopsida.

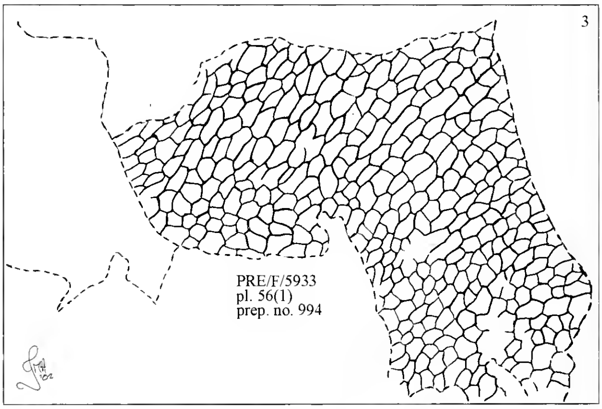
Affiliations—The cuticular correspondence between this male strobilus and the leaf *Dejerseya* (pp. 186, 187; also see And. & And. 1989, p. 258) is so close that they most probably came from the same parent-plant genus.

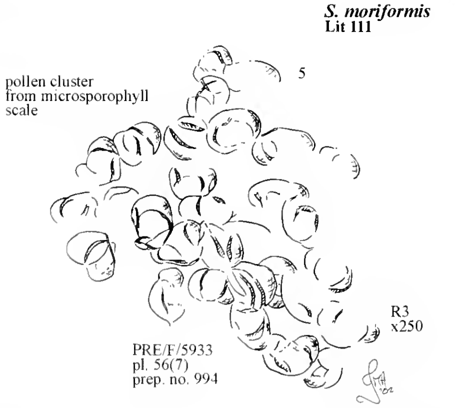
Pollen

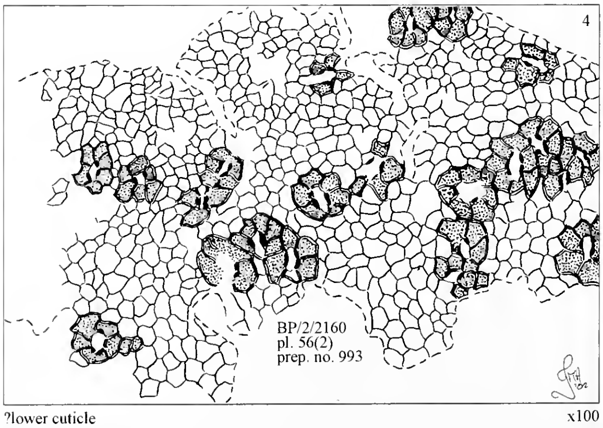
In an attempt to better classify this cone, some of the scales from Lit 111 were macerated and, most unexpectedly, disaccate pollen in aggregated masses was found. The pollen occurs in definite clusters, but no sac-like structure has been isolated. It remains uncertain whether the microsporangia occur adaxially (as preferred here) or abaxially. If the latter, then these pollen cones are particularly suggestive of the Cycadopsida and Pinopsida. The pollen sacs so characteristic of a number of the Molteno ginkgoopsid male genera (i.e. *Antevsia*, *Stachyopitys*, *Pteruchus* and *Kannaskoppianthus*) are not at all evident. However, the cuticle structure and nature of the cutinised stoma with lappetate subsidiary cells is typical for Ginkgoopsida and tends to confirm the affiliation with *Dejerseya* leaves. The cones from the three further localities (Aas 411, Mat 111, Win 111) do not have cuticle for comparison.



?upper cuticle







?lower cuticle x100

Switzianthus moriformis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: BP/2/2165 a,b; pl. 54(6, 8).
Assemblage (TC): Lit 111 Dic/Hei, Little Switzerland.
Preservation: complete cone with free axis, part and counterpart, longitudinal external view, outline of scales unclear; compression, in thinly laminated carbonaceous (good cuticle), dark grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 50 indivs (all intact), pls 54, 55.

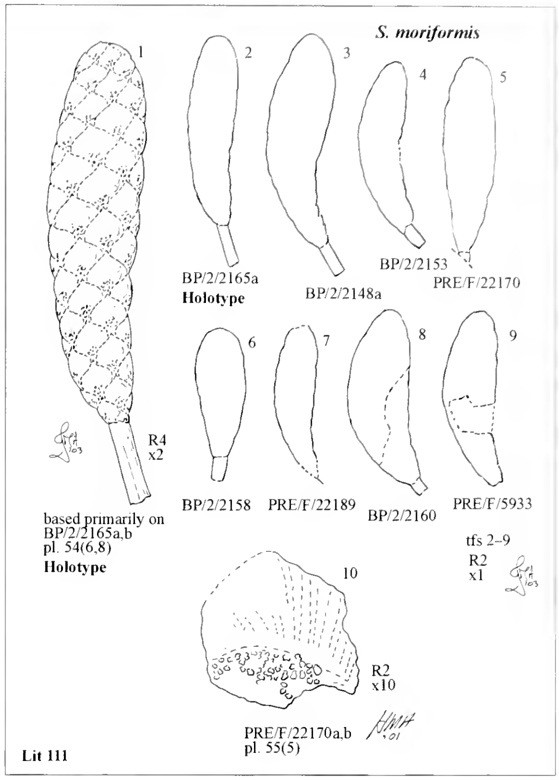
Sister palaeodemes—nil.

Specific diagnosis
A *Switzianthus* species of small size with indistinctly defined, possibly fleshy, microsporophyll scales.

Specific characters
Strobilus: cone small (*ca* 35 mm long); microsporophylls *ca* 8–10 per gyre.
Microsporophyll: scale possibly fleshy (*ca* 3 x 2.4 mm), margins of distal lamina indistinct.

Etymology
moriformis—*morus* (Lat.), mulberry.

Comment & comparison
S. moriformis is based on a single particularly well represented palaeodeme of 50 individuals, eight of which are illustrated adjacent (tfs 2–9). Though the compression material does not show the scale lamina in clear definition, it has yielded excellently preserved cuticle and *in situ* pollen grains. The species gives a fleshy appearance, with the scales seemingly coherent or semicoherent.



Switzianthus crispiformis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/12935 a,b; pl. 57(1–5).
Assemblage (TC): Aas 411 Dic/Sph, Aasvoëlberg.
Preservation: almost complete cone without free axis, longitudinal external view; 3D impression, in thinly laminated, strongly baked, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 2 indivs (1 intact, 1 partial), pl. 57(1–5).

Sister palaeodemes—2 (both listed)
Mat 111 Dic dub: 1 indiv. (intact with stalk).
Win 111 Hei elo: 1 indiv. (intact without stalk).

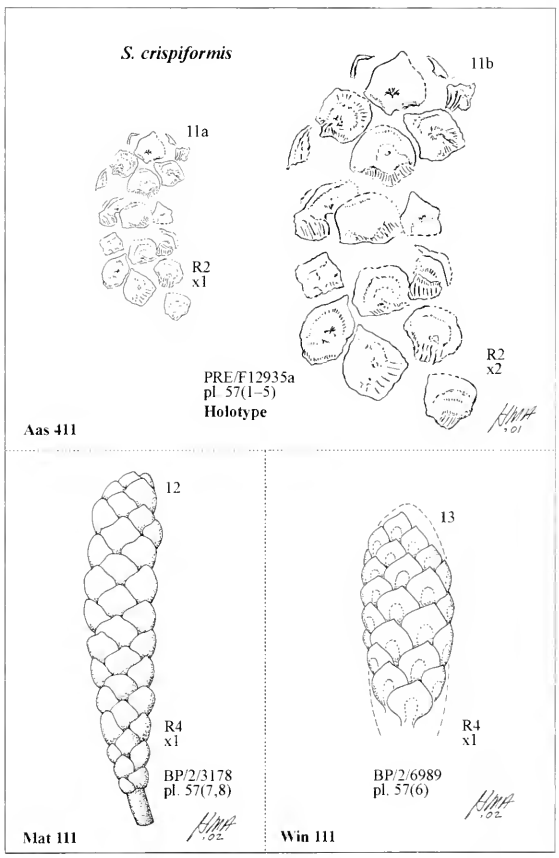
Specific diagnosis
A *Switzianthus* species of moderate size with sharply defined, possibly woody, microsporophyll scales.

Specific characters
Strobilus: cone medium-sized (up to perhaps 50 mm long); microsporophylls *ca* 6 per gyre.
Microsporophyll: scale possibly woody (*ca* 5 x 6 mm), margins of distal lamina sharply defined.

Etymology
crispiformis—*crispus* (Lat.), crisp.

Comment & comparison
Although based on a reference palaeodeme of only two specimens, *S. crispiformis* is confidently recognised as a distinct species. It is larger than *S. moriformis* (from Lit 111) and the scales are very much more sharply defined. The single specimens (tfs 12, 13 adjacent) from Mat 111 and Win 111 are included here with much reservation: they may equally well represent two additional species.

It is quite possible that *S. crispiformis* should be transferred to the cycadopsid genus *Androstrobus*: in view of this uncertainty the generic diagnosis of *Switzianthus* is based exclusively on *S. moriformis*.



Dejerseya R.Herbst 1977

Type species
Dejerseya lunensis (Johnston) And. & And. 1989.
Southport, near Ida Bay, Tasmania, Australia; Carnian, Triassic.

Generic concept
A ginkgoopsid leaf with linear to elliptic, simple to deeply lobed lamina.

Generic characters (Molteno Formation)
Leaf: medium-sized, linear to broadly elliptic; lamina margin ranging from entire to gently sinuate to lobed to almost pinnate; apex obtuse; petiole indistinct; venation pattern dependent on degree of lobing, midrib prominent; secondary veins arching at 30–60°, forking several times.
Cuticle: see And. & And. (1989, p. 258), this vol., tfs 12–15 below.

Eponymy
Dejerseya—for Dr N.J. de Jersey, Queensland palynologist and palaeobotanist.

Global range: 1 sp., Gondwana Tr. (CRN).
First & last: *Dejerseya lunensis* (And. & And. 1989, p. 258); Molteno Fm., S. Africa; Blackstone Fm., Ipswich Basin, Australia.

Gondwana Triassic occurrence
Frequency (F): 7 degree squares (of the 84 across Gondwana).
Ubiquity (U): 2 continents (of 5 comprising Gondwana).
Diversity (D): 1 species.
Abundance (A): 11% (the norm in Molteno TCs).
Longevity (L): 2 myrs (Lower Carnian).

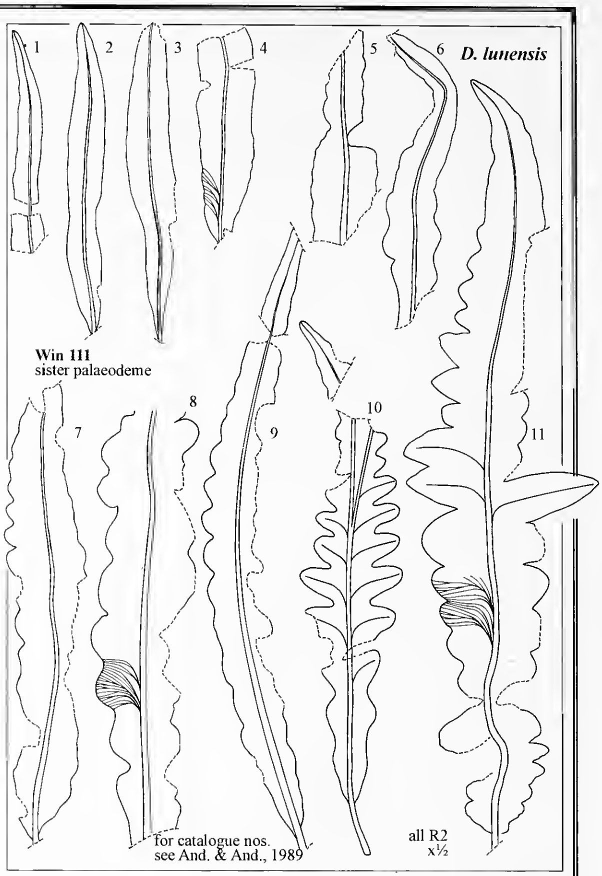
Colonisation success: FUDAL rating 7/2/1/11/2 = 23.
Limited success (Grade 2): *Dejerseya* was the 15th most prominent genus in the Gondwana Triassic; it was relatively abundant where it occurred, but was infrequent and included only a single very variable species.
Endemism: the genus, as currently known, shows a clearly disjunct distribution both in Gondwana (Karoo Basin, Clarence-Moreton Basin, Tasmania) and within the Karoo (three widely separated TCs).

Molteno occurrence
Frequency (F): 5 TCs (of 100 sampled in the Molteno).
Diversity (D): 1 species (with much intraspecific variation).
Abundance (A): co-dominant (20%) in 2 TCs; occasional to abundant (2–10%) in 2 TCs, rare (<1%) in 1 TC.

Habit: possibly a small spreading tree.
Preferred habitat: *Heidiphyllum* thicket.

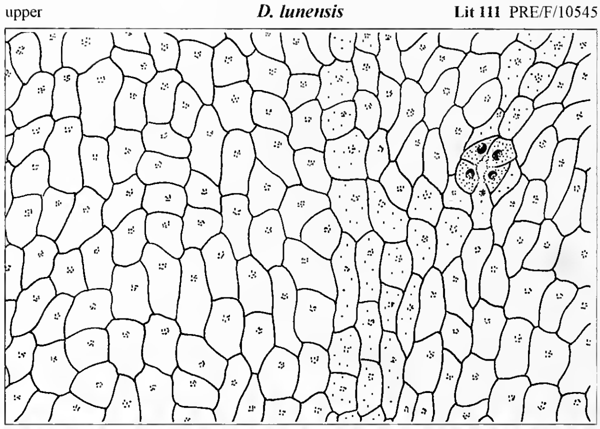
Affiliated organs
Female strobilus: see discussion on p. 182.
Male strobilus: *Switzianthus*—Grade 3 (Cut. cor., Mut. occ.).

Classification & comparison
Intergeneric comparison
Dejerseya resembles some *Dicroidium* species, e.g. *D. coriacium*, in its essentially nonpinnate laminae and the venation, but differs in its unforked frond. The cuticle, with variously distant to proximate lappets and distinctively striate guard cells, distinguishes *Dejerseya* from all other Gondwana ginkgoopsid genera.
Interspecific comparison
At present, *Dejerseya* is regarded as a single, highly polymorphic species. It is known from five TCs in the Molteno Fm. and seven in Australia.

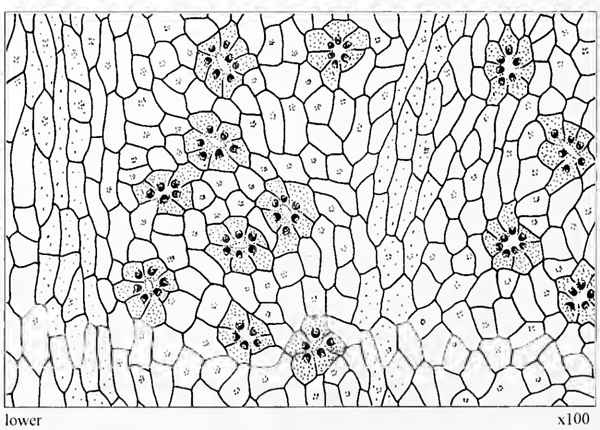


upper *D. lunensis* **Lit 111** PRE/F/10545

12

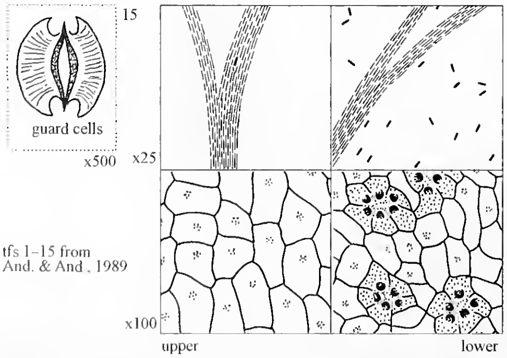


13



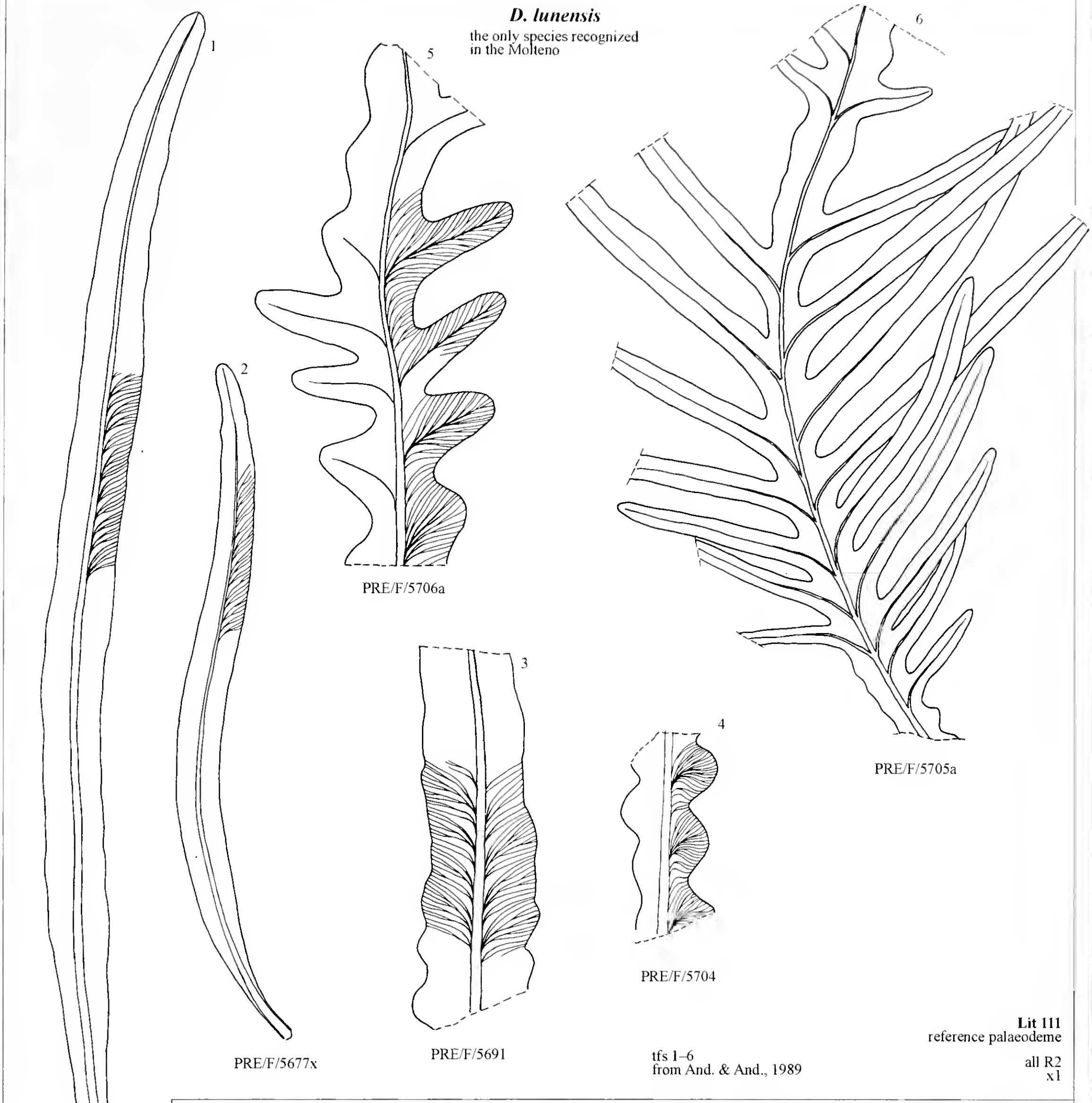
lower x100

D. lunensis
Lit 111 PRE/F/10545



tfs 1–15 from And. & And., 1989

D. lunensis
the only species recognized in the Molteno



PRE/F/5706a

PRE/F/5705a

PRE/F/5704

PRE/F/5645

PRE/F/5677x

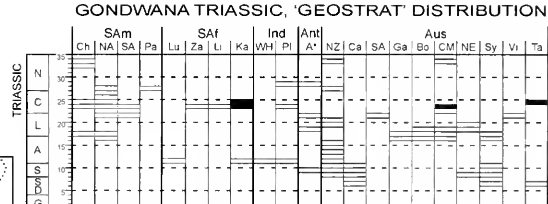
PRE/F/5691

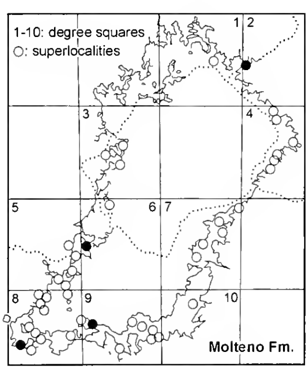
tfs 1–6
from And. & And., 1989

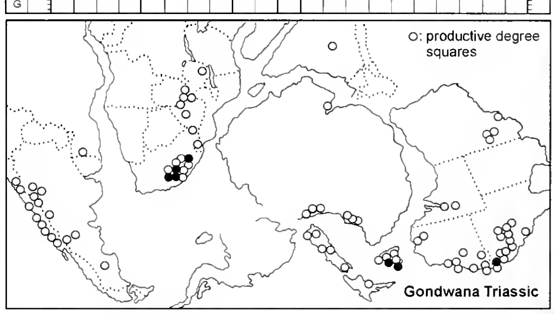
Lit 111
reference palaeodeme

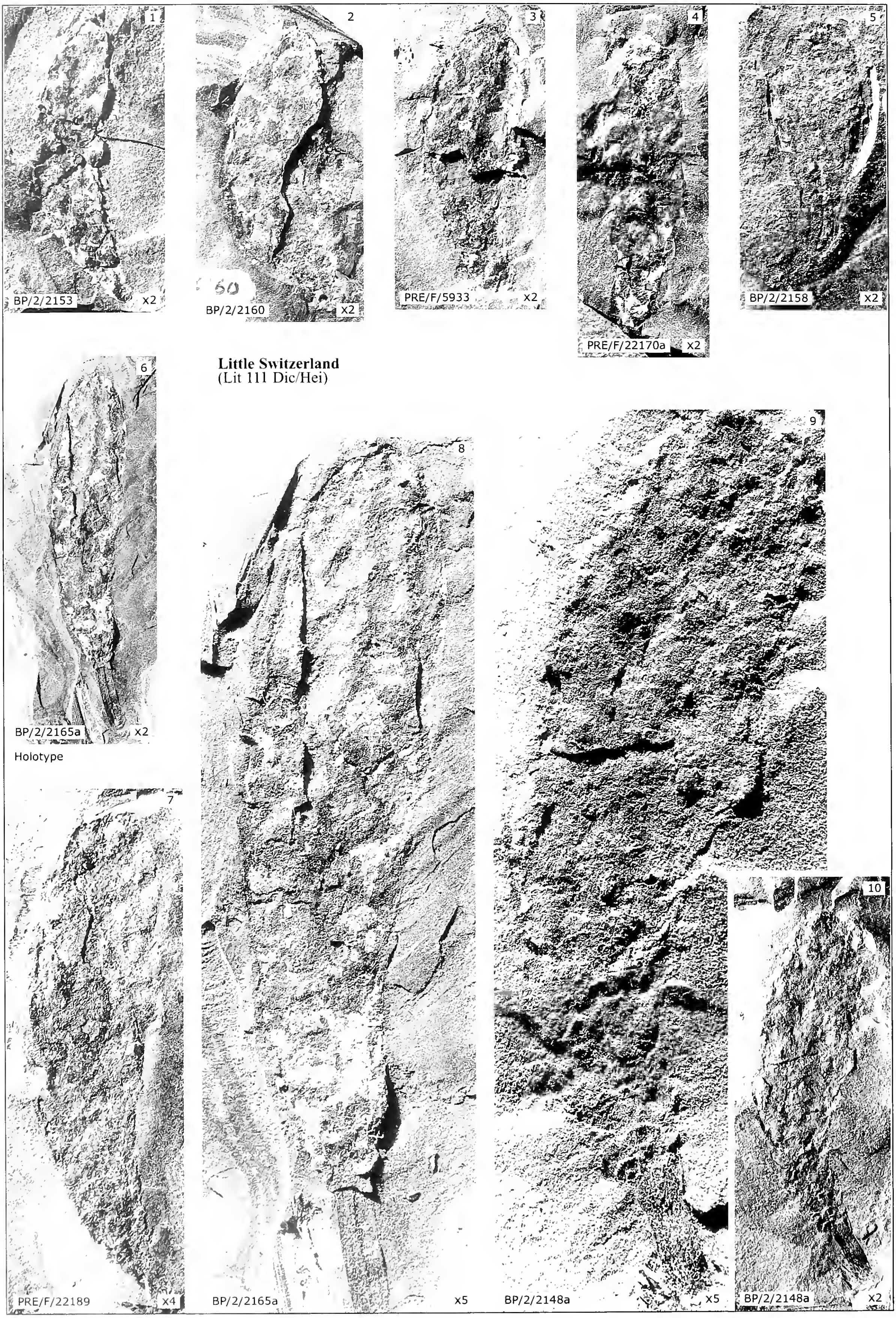
all R2
x1

GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION

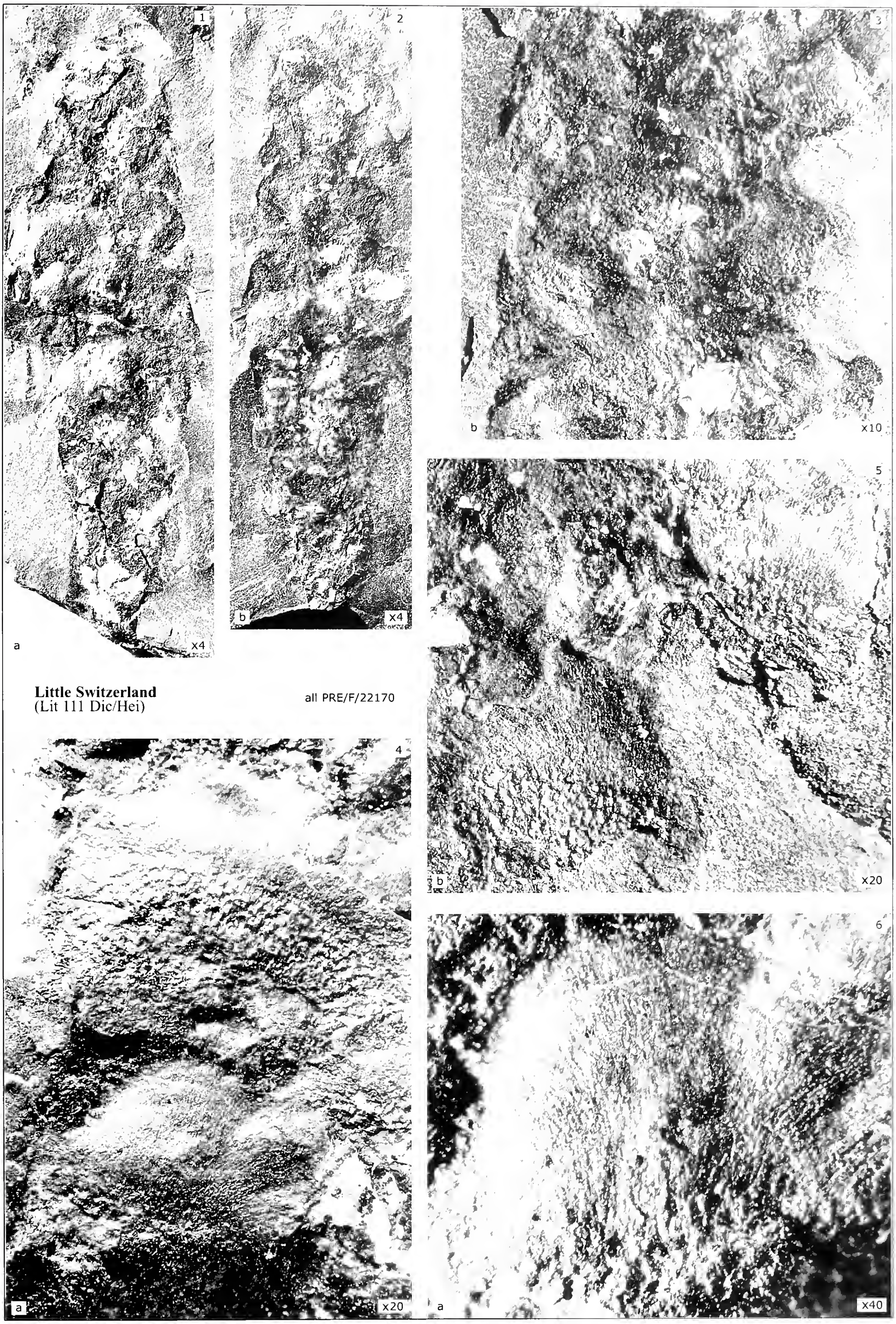






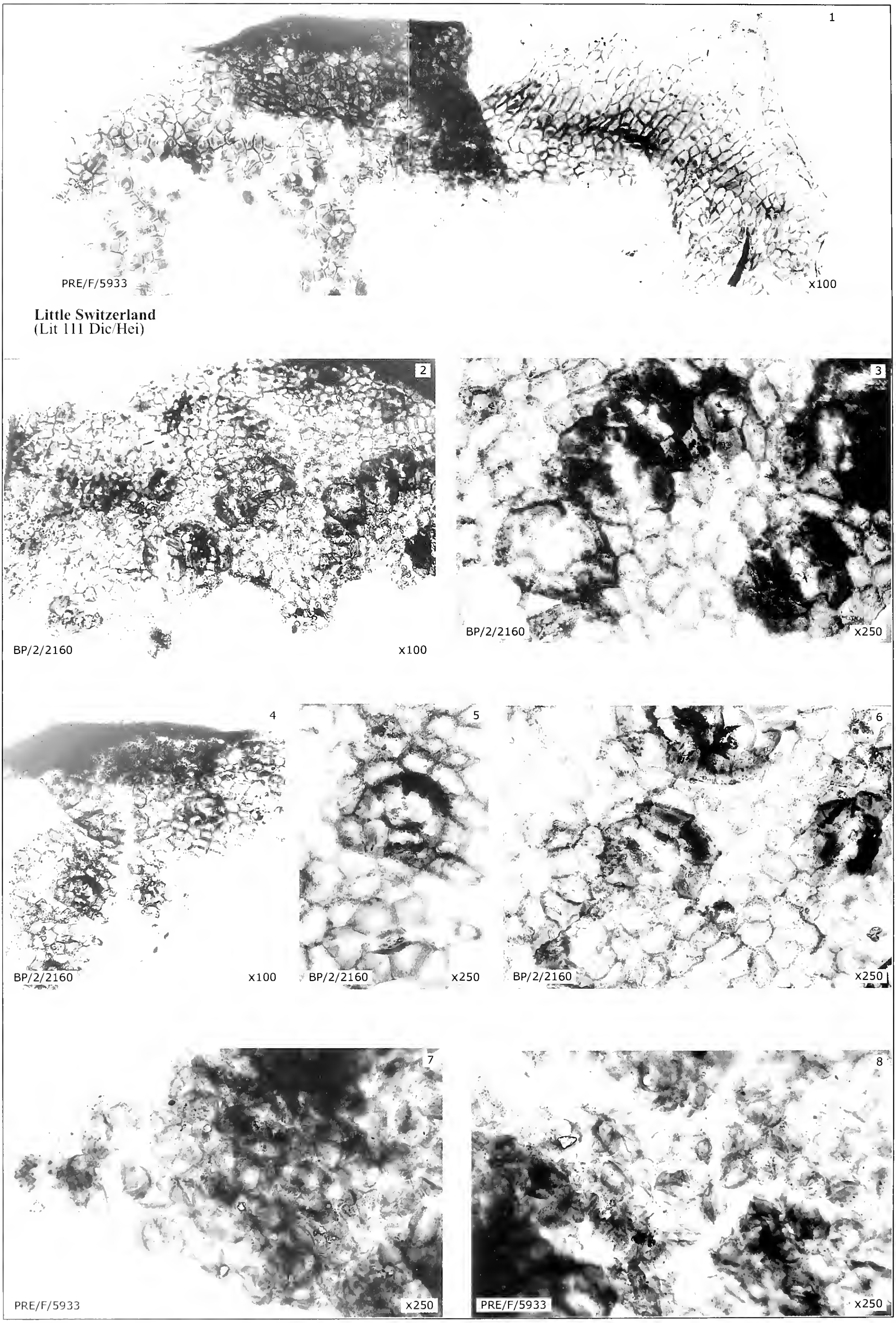


Switzianthus moriformis **pl. 54** **MATATIELLALES**

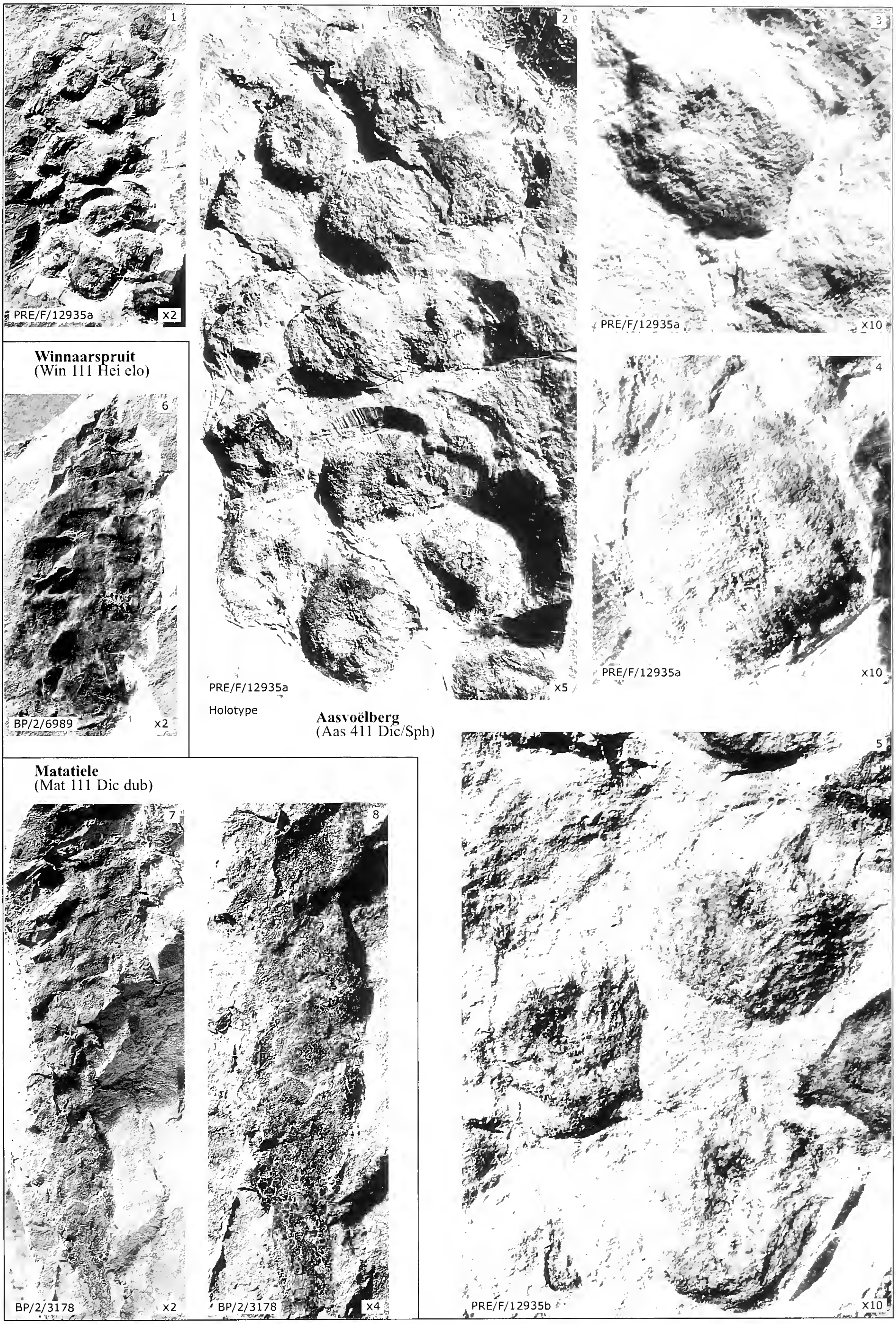


Little Switzerland
(Lit 111 Dic/Hei)

all PRE/F/22170



Switzianthus moriformis **pl. 56** **MATATIELLALES**


1
PRE/F/12935a
x2
2
PRE/F/12935a
Holotype
x5
3
PRE/F/12935a
x10
4
PRE/F/12935a
x10
Winnaarspruit
(Win 111 Hei elo)
6
BP/2/6989
x2
Aasvoëlberg
(Aas 411 Dic/Sph)
5
PRE/F/12935b
x10
Matatiele
(Mat 111 Dic dub)
7
BP/2/3178
x2
8
BP/2/3178
x4

GINKGOOPSIDA S.V.Meyen 1984
GINKGOALES Engl. 1897
AVATIACEAE J.M.And. & H.M.And., fam. nov.

Avatia J.M.And. & H.M.And., gen. nov.

Type species
Avatia bifurcata J.M.And. & H.M.And., sp. nov.
Birds River, Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis
A ginkgoopsid strobilus consisting of a simple, once-forked axis bearing a pair of megasporophylls each consisting of a single, erect, leafy, shallowly lobed, palmate, multiovulate head.

Generic characters
Strobilus: simple, lax, bilaterally symmetrical, small (*ca* 20–25 mm long); axis gracile, elongate, distally forked; megasporophylls a single distal pair.
Megasporophyll: simple, pedunculate; multiovulate heads palmate (6 x 8 mm), shallowly 4–6-lobed; ovules/seeds readily dehisced, one per lobe.
Ovule/seed: irregularly oval to elliptical (*ca* 4 x 2 mm), narrowly winged, with characteristic elliptical scars (possibly fungal).

Etymology
Avatia—*Avis* (Lat.), bird, after the type locality Birds River.

Global range: 1 sp., Gondwana, Tr. (CRN).
First & last: the Molteno species described here.

Gondwana Triassic occurrence
SAf—Karoo Basin, 6 TCs (>110 indivs).

Molteno occurrence
Frequency (F): 6 TCs (of 100 sampled in Molteno).
Diversity (D): 1 species.
Abundance (A): >110 individuals, rare to very rare.

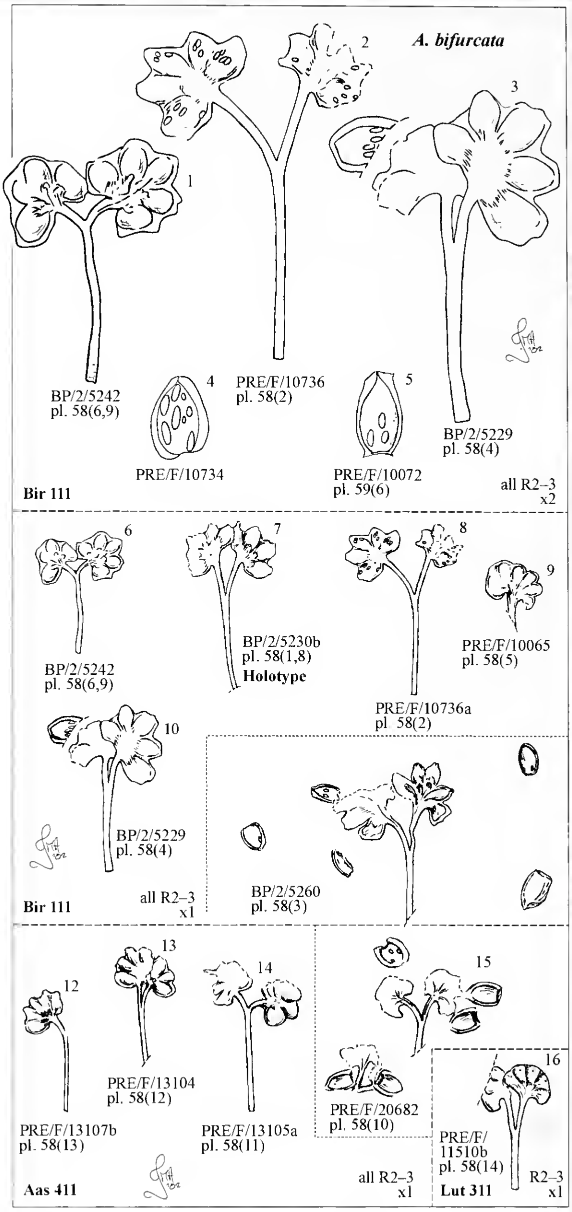
Bir 311 Hei/Sph:	1 indiv in	2 man-hrs cleaving	(5 per	1 man-day)	rare	
Nuw 111 Dic zub:	5 " "	21 " "	(3 "	1 ")	"	
Aas 411 Dic/Sph:	38 " "	512 " "	(>1 "	1 ")	"	
Bir 111 Sph 2spp:	66 " "	550 " "	(>1 "	1 ")	"	
Tin 121 Sph 2spp:	1 " "	5 " "	(2 "	1 ")	very rare	
Lut 311 Hei elo:	3 " "	50 " "	(1 "	2 ")	"	"

The figures for Bir 111 and Aas 411 refer only to curated individuals—a selection of the best specimens from the site. The rate of yield of *Avatia* at these two TCs is, in reality, much higher.

Affiliated organs
Male strobilus: *Eosteria*—Grade 3 (Kin. reinf., Mut. occ.).
Foliage: *Ginkgoites*—Grade 2 (Mut. occ.).

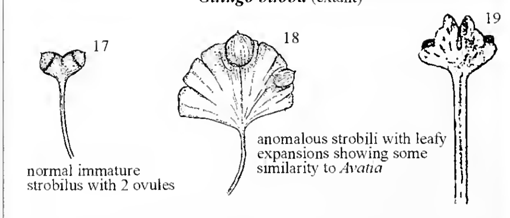
Classification & comparison
Suprageneric classification (*Avatiaceae/Ginkgoales*)
In view of the generalised similarities between *Avatia* and the extant *Ginkgo* female strobilus (see box opposite), the probable affiliation with *Eosteria* (comparable to the male strobilus of modern *Ginkgo*), and the most-likely affiliation with *Ginkgoites* leaves, we include *Avatia* in the order Ginkgoales. However, the difference between *Avatia* and *Ginkgo* (ovulate strobilus) is sufficiently great to warrant placing the former in a new family (Avatiaceae). It is essentially in the number of ovules per ovuliferous head that the divergence in morphology lies.

Intergeneric comparison (Gondwana Triassic)
An intriguing and varying range of similarities occur between *Avatia* and the other ovulate ginkgoopsid genera found in the Molteno. *Fanerotheca*, with the winged seed *Feruglioa*, bears 4-lobed cupules, but these occur in multiple pairs along megasporophylls attached to a full strobilus. *Umkomasia*, in some species, bears once-forked megasporophylls, but these do not have palmate heads. *Peltaspermum* is characterised by peltate, multilobed ovulate heads that readily detach. *Matatiella* has a similar palmate megasporophyll, but it is deeply lobed and attached helically to an axis. *Hamshawvia* has a once-forked strobilus with a pair of megasporophylls, but these are fleshy and with 8 to 16 small ovules.



Reconstructions
We have attempted no more than R2–3 reconstructions of *Avatia* from the reference palaeodeme, Bir 111, or the sister palaeodemes, Aas 411 and Lut 311 (see above). While there is good evidence that the seeds shown are affiliated with *Avatia*, it is unknown whether they are attached adaxially, abaxially, or enclosed within the megasporophyll lobe.

Ginkgo biloba (extant)



tfs 17,18 from Krassilov (1972)
tf. 19 from Seward & Gowan (1900)
all *ca* x1½

Evidence for affiliation of organs

Kindred reinforcement

Avatia resembles the extant *Ginkgo* strobilus in its typical pair of ovules (tfs 1–16 opposite). There are also similarities with some of the anomalous forms of *Ginkgo* strobili (tfs 18, 19 opposite) as reported by Seward & Gowan (1900, fig. 37) and Krassilov (1972, fig. 1a, b). See Hara (1997) for a recent discussion and further examples of anomalous strobili. However, the fleshy fruit and hard pip of *Ginkgo biloba* is quite unlike the palmate head and winged seed of *Avatia*.

Mutual occurrence

Foliage—Ginkgoites occurs frequently at Bir 111 and Aas 411 and is the most likely nominee for affiliation with *Avatia* (Grade 2). It is absent from Lut 311 and Nuw 111 (Tab. 46). If *Sphenobaiera* was not already pre-occupied (Grade 3 affiliation with *Hamshawvia*), it would be a more or less equal candidate for affiliation with *Avatia*. The immature female strobilus attached to the short shoot with *Sphenobaiera* [p. 223, tf. 10; pl. 71(1–4)], while difficult to identify, could also be *Avatia*. No other gymnospermous foliage in the Molteno shows a pattern of occurrence suggesting any likely link with *Avatia*.

Male—Eosteria; see discussion under that genus (p. 196).

Seeds—A distinctive narrowly winged seed (pl. 59) co-occurs with *Avatia* in the three TCs listed below, suggesting an affiliation of Grade 3 reliability. This affiliation is supported by the presence of the elliptical scars, possibly of fungal origin, that occur on both the seeds and the megasporophyll lobes.

Bir 111—Numerous seeds occur either scattered or in dense clusters, pl. 58(7), and in several cases, pl. 58(3, 4), they lie in close proximity to *Avatia* megasporophylls, but, unfortunately, are never found attached. The elliptical scars which are very evident on the seeds, pl. 59(4–9), are seen also in one of the illustrated palmate heads, pl. 59(2).

Aas 411—One slab, PRE/F/20682, pl. 58(10), has two *Avatia* individuals with the affiliated seeds in close proximity as if they may have been attached in life.

Nuw 111—Three of the five megasporophyll-bearing slabs show several dispersed seeds. None of these are attached or bear the characteristic elliptical scars. Numerous slabs show only dispersed seeds.

assemblages (taphocoenosis)		*Ginkgoites*	*Paraginkgo ant.*	*G. koningensis*	*waldeckensis*	*matatiensis*	*aviamnica*	*muriselmata*	*telemachus*	♀ inflor. *Avatia*	♀ seeds	♂ *Eosteria*	*E. eosteranthus*	*telemanthus*
Bir 211	Sph 2spp	3	-	-	-	3	-	-	-	-	-	-	-	-
311	Hei/Sph	1	-	-	-	1	-	-	-	1	-	-	-	-
111	Sph 2spp	43	-	-	-	35	8	-	-	66	✓✓✓	5	5	-
Gre 111	Sph pon	**5**	-	-	-	**5**	-	-	-	-	-	-	-	-
"	Equ sp	1	-	-	-	1	-	-	-	-	-	-	-	-
Tel 111	Hei elo	23	-	-	-	-	-	-	23	-	-	8	-	8
Vin 111	Dic odo	**1**	-	-	-	**1**	-	-	-	-	-	-	-	-
Ela 111	"	**3**	-	-	-	**3**	-	-	-	-	-	-	-	-
Lut 311	Hei elo	-	-	-	-	-	-	-	-	3	3?	2	2	-
Tin 121	Sph 2spp	-	-	-	-	-	-	-	-	1	-	-	-	-
Wal 111	Dic odo	**2**	-	-	**2**	-	-	2	-	-	-	-	-	-
Kon 223	"	4	-	1	-	3	-	-	-	-	-	-	-	-
222	"	13	-	13	-	-	-	-	-	-	-	-	-	-
Nuw 111	Dic zub	-	-	-	-	-	-	-	-	5	✓✓	-	-	-
211	Dic 2spp	**1**	-	-	-	**1**	-	-	-	-	-	-	-	-
Maz 111	Dic cra	1	-	-	-	1	-	-	-	-	-	-	-	-
211	Hei/Dic	3	-	-	-	3	-	-	-	-	-	-	-	-
San 111	Dic cra	5	3	-	-	5	-	-	-	-	-	-	-	-
Mng 111	Dic 2spp	2	-	-	-	2	-	-	-	-	-	-	-	-
Mat 111	Dic dub	25	-	-	-	25	-	-	-	-	-	-	-	-
Lit 111	Dic/Hei	4	40	-	-	3	-	-	1	-	-	-	-	-
Aas 311	Hei elo	-	-	-	-	-	-	-	-	-	-	12	12	-
411	Dic/Sph	20	-	-	-	20	-	-	-	38	7	-	-	-
Total TCs		19	2	2	1	16	1	1	2	6	4	4	3	1
Total indivs		%	43	14	%	%	8	2	24	114	✓	27	19	8

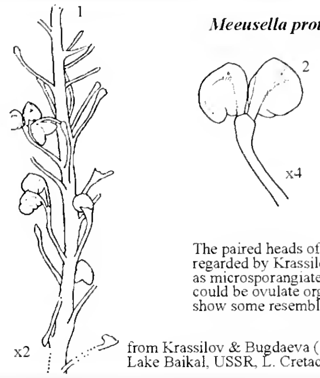
Tab. 46. ***Avatia/Ginkgoites*, Molteno occurrence**

Abundance: individuals of *Avatia* are abundant at both Bir 111 and Aas 411. In these TCs only the number of curated specimens is recorded. Many further isolated individuals occur on other slabs in the collection.

Comparisons beyond Gondwana Triassic

The ovulate organs from outside the Gondwana Triassic most similar to *Avatia* are the glossopterid genera *Rigbya* and *Lidgettonia* from the Gondwana Permian (And. & And. 1985, pp. 127–136). These both have lobed megasporophyll heads, apparently bearing winged seeds. Though neither are forked like *Avatia*, either could have evolved over a geological period to look similar. The seeds affiliated here with *Avatia* are, in hand specimens, closely similar to those that have been affiliated with another putative glossopterid ovulate fruit, *Arberia* (And. & And. 1985, pp. 128–131).

Zhou (1991, 1997) reviewed ginkgoalean female megafossils attached or affiliated with *Ginkgo* fossil leaves. None of these, e.g. *Karkenia* (Lower Cretaceous, Tico Flora, Santa Cruz Province, Argentina), *Yimaia* (Middle Jurassic, Yima Fm., Henan, China) and *Umaltolepsis* (Upper Jurassic & Lower Cretaceous, Bureja River Basin, Siberia), show a resemblance to *Avatia*.



The paired heads of *Meeusella* were regarded by Krassilov and Bugdaeva as microsporangiate. However, they could be ovulate organs and they do show some resemblance to *Avatia*.

from Krassilov & Bugdaeva (1988) Lake Baikal, USSR, L. Cretaceous

Avatia bifurcata And. & And., sp. nov.

Holotype

Specimen: BP/2/5230a,b; pl. 58(1, 8).

Assemblage (TC): Bir 111 Sph 2spp, Birds River.

Preservation: virtually complete strobilus, part and counterpart; impression in thinly laminated, yellowish grey shale with very good cleavage.

Reference palaeodeme (Molteno Fm.)

Assemblage (TC): as for holotype.

Specimens: 66 indivs (most intact), pls 58(1–9), 59(1–9).

Sister palaeodemes (Molteno Fm.)—5 (best 1 listed)

Aas 411 Dic/Sph: 38 indivs.

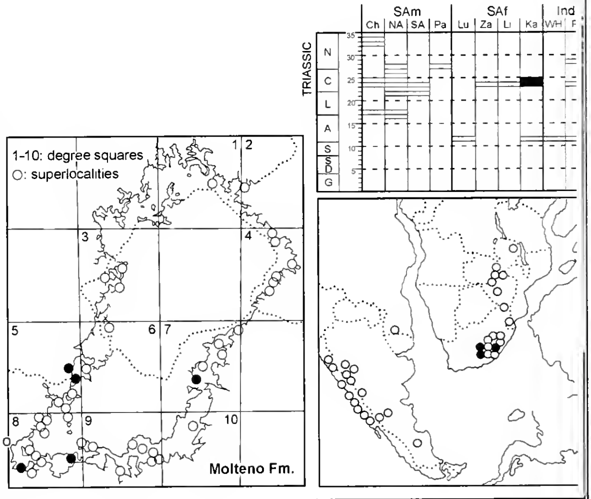
Specific diagnosis: as for genus.

Diagnostic characters: as for genus.

Etymology

bifurcata—with reference to the bifurcating form of the strobilus.

Classification & comparison: see under genus.



Eosteria J.M.And. & H.M.And., gen. nov.

Type species
Eosteria eosteranthus J.M.And. & H.M.And., sp. nov.
Aasvoëlberg (Aas 311), Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis
A ginkgoopsid male strobilus of linear, spicate form, with simple microsporophylls comprising single, pedunculate microsporangiate cupules.

Generic characters
Strobilus: simple, linear spicate, relatively lax, radially symmetrical, small (up to *ca* 40 mm long); axis gracile, gently sinuous to erect; microsporophylls numerous, helically arranged.
Microsporophyll: simple, pedunculate; peduncle gracile (*ca* 1 mm long); microsporangia borne singly.
Microsporangium: cupulate, bilaterally symmetrical; closed sac ovoid (*ca* 2–3 mm long), opened sac relatively deeply 6-lobed.
Pollen: monosulcate, spherical with large circular germinal furrow.

Etymology
Eosteria—after a Germanic goddess *Eostre*; with reference to the type locality Aasvoëlberg (Aas 311), informally called 'Easter Egg Shale'.

Global range: 2 spp., Gondwana, Tr. (CRN).
First & last: the 2 Molteno species described here.

Gondwana Triassic occurrence
SAf—Karoo Basin, 4 TCs (27 indivs).

Molteno occurrence
Frequency (F): 4 TCs (of the 100 Molteno TCs sampled).
Diversity (D): 2 species.
Abundance (A) 27 indivs total, very rare to extremely rare.

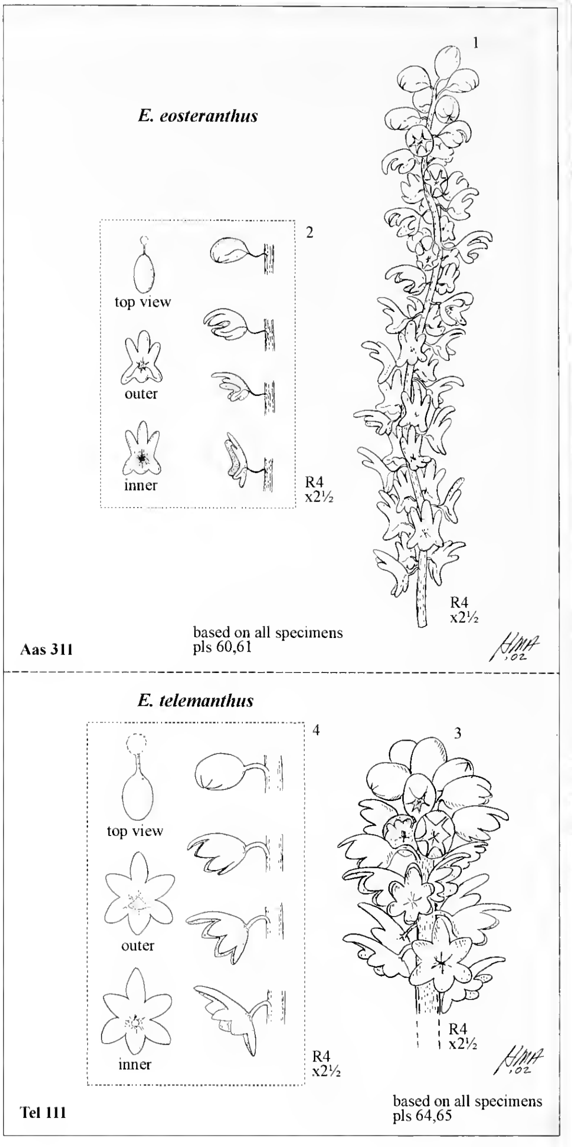
Aas 311 Hei elo:	12 indivs in	140 man-hrs cleaving	(1 per	1 man-day)	very rare
Tel 111 Hei elo:	8 " "	90 " "	(1 "	1 ")	"
Lut 311 Hei elo:	2 " "	50 " "	(1 "	2 ")	"
Bir 111 Sph 2spp:	5 " "	550 " "	(1 "	11 ")	extr. rare

Eosteria is an infrequent and very rare element in the Molteno.

Affiliated organs
Female strobilus: *Avatia*—Grade 3 (Kin. reinf., Mut. occ.).
Foliage: *Ginkgoites*—Grade 3 (Kin. reinf., Mut. occ.).

Classification & comparison
Suprageneric classification (Avatiaceae/Ginkgoales)
As discussed earlier (p. 192), the plant-genus comprising the affiliated grouping of *Avatia* (female), *Ginkgoites* (foliage) and *Eosteria* (male), is readily placed in the order Ginkgoales. Of all the Molteno microsporangiate genera, *Eosteria* is clearly most like the male strobilus of the extant *Ginkgo biloba* (box on p. 195). In our view, both *Avatia* and *Eosteria* are sufficiently different from their living female and male ginkgoalean counterparts, however, to warrant including them in a distinct family (Avatiaceae).

Intergeneric comparisons (Gondwana Triassic)
The other ginkgoopsid microsporangiate genera from the Molteno—*Antevsia*, *Switzianthus*, *Stachyopitys*, *Pteruchus* and *Kannaskoppianthus*—are all fundamentally different from *Eosteria*. None consists of a spicate strobilus or bears cupulate microsporangia remotely like it.



Reconstructions
Strobilus
The R4 strobilus reconstructions of the two described species, *E. eosteranthus* and *E. telemanthus*, are based on the full set of specimens in the reference palaeodeme of each. For both species, the holotype is used as the basis for overall size and shape, but other individuals are referred to for details of the microsporophylls and their attachment. The full length of the strobilus is uncertain for both species. We have chosen to show the strobili with fully open sacs proximally and with closed sacs distally.

Microsporangia
Interpretation of the structure of the individual microsporangial sacs is particularly difficult. In *E. telemanthus*, for instance, there is only one specimen [PRE/F/17330a'y', pl. 65(1–3); this lies immediately adjacent to the holotype on the same slab] with a single opened sac that shows most of the lobes and their margins intact. The next most fully preserved open sac is that towards the proximal end of the holotype [PRE/F/17330a,b'x', pl. 64(1, 5)] and this gives a quite contradictory impression of shape. The outer margins of the lobes angle upwards out of the sediment and are torn. Similarly for *E. eosteranthus* from Aas 311: only in PRE/F/22074 [pl. 61(4)] is there an open sac with the distal lobes untorn, while other specimens, e.g. PRE/F/22067, pl. 61(5–7); PRE/F/22070, pl. 60(1–5), show open sacs with torn margins that suggest different shapes. The closed or partially open sacs are most evident in Lut 311 (pl. 62) and Bir 111 (pl. 63).

Extant *Ginkgo biloba* (male strobilus)

Ginkgo biloba bears a simple linear male strobilus with numerous spirally arranged microsporophylls on slender pedicels. The microsporangia, however, are rather distinct: they consist of a closed pair of linear-oblong sacs suspended from a flattened receptacle at the end of the pedicel; the sacs dehisce along an inner suture to release the pollen. The dried, opened pair of sacs distort irregularly to present a variety of shapes. Pollen is found adhering in abundance to the hirsute inner face of the sacs.

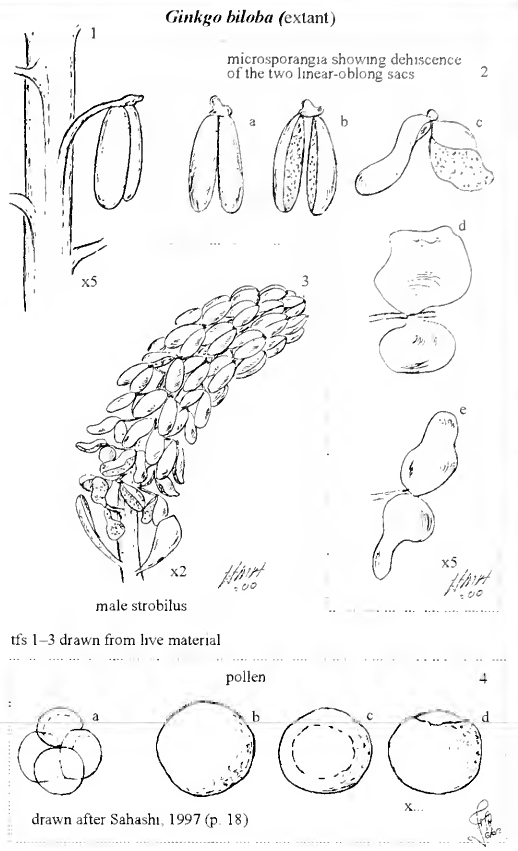
Eosteria & G. biloba

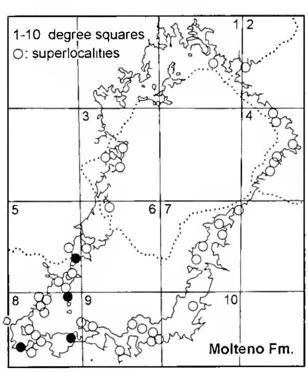
Eosteria is closely similar to the extant *Ginkgo* male in its simple strobilus with spirally arranged microsporophylls borne on slender pedicels, but differs in its single microsporangium (not paired) and the sac dehiscing into *ca* six lobes (not a single suture). Both genera yield monocolpate pollen.

Ginkgoales

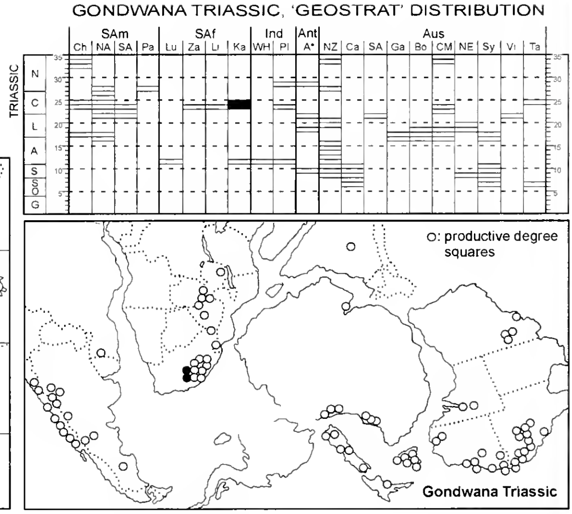
Evidence of the male strobilus of *Ginkgo* in the fossil record is particularly sparse. Only four references are known to us:

- Harris & Millington (1974); Yorkshire Jurassic; 1 individual.
- Schweitzer (1977); Alborz Mountains, Rhaetic, Iran, *ca* 8 individuals; *Irania* (Iraniales). *I. hermaphroditica* is an axis bearing male and female strobili (the latter on the upper part of the axis). The microsporophyll strobilus is very similar to the extant *Ginkgo biloba* male strobilus with two pollen sacs per microsporangium. So far no pollen grains have been found. The combination of male and female in one structure makes *Irania* a unique organ and its classification an enigma.
- Drinnan & Chambers (1985, 1986), Douglas (1969); Koonwarra Lake deposit in Whitelaw road cutting, Victoria, mid-Cretaceous; four specimens, two being multiple and attached to an axis.
- Rothwell & Holt (1997); central Alberta, Upper Cretaceous, one individual.



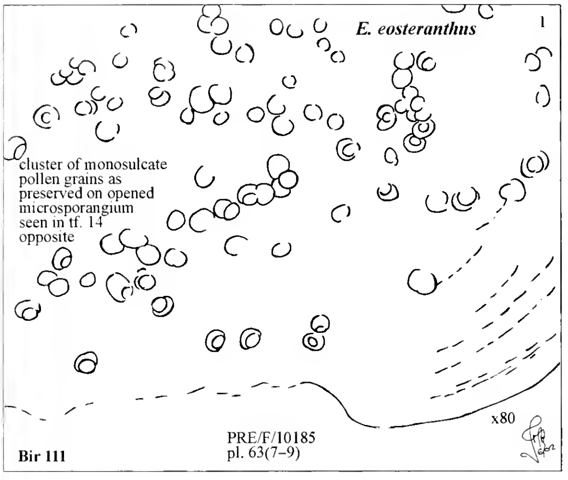


GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION



Pollen

Three specimens, one each from Aas 311 [PRE/F/22070, pl. 60(1–5)], Tel 111 [PRE/F/17325, pl. 65(5–7)] and Bir 111 [PRE/F/10185, pl. 63(7–9)], show *in situ* clusters of pollen in opened or naturally sectioned microsporangial sacs. The most clearly preserved of these clusters is that from Bir 111, where, at ∞80 magnification, it is quite evident that the grains are spherical with a large rounded germinal furrow. They compare very closely to those of extant monocolpate pollen of *Ginkgo biloba* (Sahashi 1997).



Evidence for affiliation of organs

A Grade 3 affiliation of *Eosteria* with the female strobilus *Avatia* and with the foliage *Ginkgoites* is based on the following evidence:

Mutual occurrence (Tab. 46)

Eosteria occurs together with *Ginkgoites* (common, two species) and *Avatia* (abundant) at Bir 111, with only *Ginkgoites* (rare, one species) at Tel 111, with only *Avatia* (rare) at Lut 311, and with neither genus at Aas 311.

Kindred reinforcement: The extant *Ginkgo biloba* male strobilus (see boxes and relevant text) is similar to *Eosteria* in both gross morphology and pollen grains.

Adaptive radiation (Molteno diveristy)

It is likely that *Eosteria* was more diverse than the available material (in quantity, intactness and clarity) enables us to recognise. While four palaeodemes are represented and only two species have been defined, we consider it more likely, in life, that four species may have been present.

The chief diagnostic characters are the shape and robustness of the strobili, and the shape and orientation of the lobes in the fully opened microsporangiate sacs.

The two species, each based on reasonably sized reference palaeodemes and deriving from the same habitat but different stratigraphic levels, are:

E. eosteranthus—Aas 311 Hei elo (Aasvoëlberg); 12 indivs
Heidiphyllum thicket; Cycle 1 (Bamboesberg Member)
E. telemanthus—Tel 111 Hei elo (Telemachus); 8 indivs
Heidiphyllum thicket; Cycle 3 (Mayaputi Member)

Eosteria telemanthus J.M.And. & H.M.And., sp. nov.

Holotype

Specimen: PRE/F/17330a,b'x'; pl. 64(1, 2, 5).
Assemblage (TC): Tel 111 Hei elo, Telemachus Spruit.
Preservation: almost complete strobilus, part and counterpart; impression in thickly laminated, light olive-grey shale with poor cleavage.

Reference palaeodeme

Assemblage (TC): as for holotype.
Specimens: 8 indivs (1 intact, 3 partial, 4 isolated), pls 64(1–8), 65(1–7).

Sister palaeodemes—nil.

Specific diagnosis

An *Eosteria* species with a relatively stout strobilus and microsporangial sacs dehiscing radially into 6 fairly equal lobes.

Specific characteristics

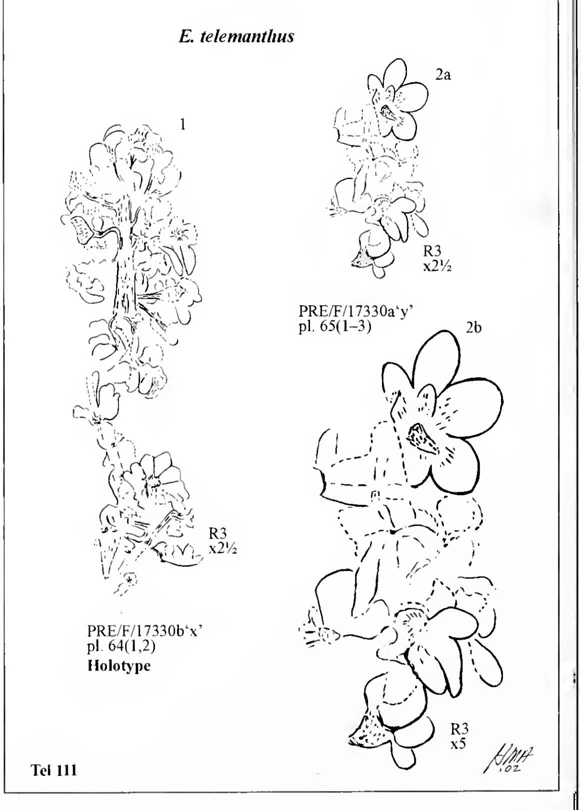
Strobilus: relatively stout (length unknown).
Microsporangium: cupulate sacs dehiscing into 6 fairly equal lobes; outer pair of proximal lobes without distinctive ribs.

Etymology

telemanthus—a male cone from Telemachus Spruit (Tel 111).

Comment & comparison

The *E. telemanthus* palaeodeme includes a number of very clearly preserved specimens. They would show up particularly well if photographed in colour—with the rust-coloured points of pedicel attachment, for instance, standing out sharply. The species appears distinct, as is its putative foliage affiliate, *Ginkgoites telemachus*, which is also well represented (23 individuals) and exclusive to Tel 111.



Eosteria eosteranthus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/19388a,b; pl. 60(6–8).
Assemblage (TC): Aas 311 Hei elo, Aasvoëlberg.
Preservation: nearly complete strobilus, part and counterpart; impression, in thickly laminated, light grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 12 indivs (3 intact, 4 partial, 5 isolated), pls 60(1–8), 61(1–7).

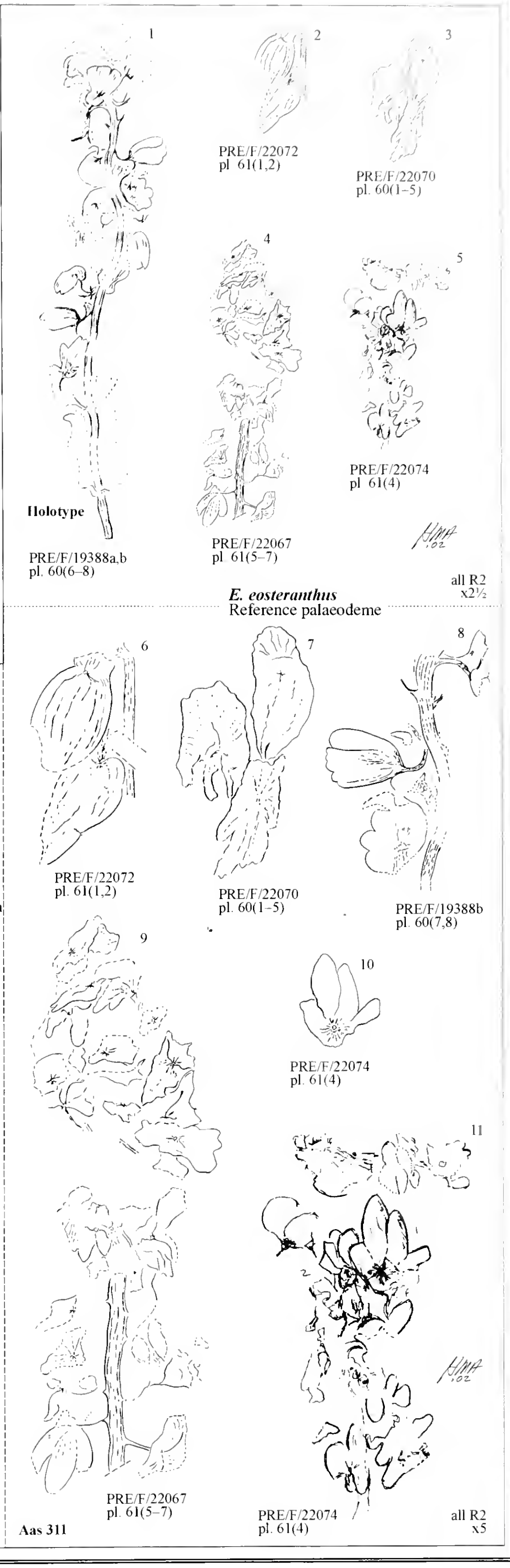
Sister palaeodemes—2 (both listed)
Bir 111 Sph 2spp: 5 indivs, distinctive pollen grains; pl. 63(1–9).
Lut 311 Hei elo: 2 indivs, clear axis and pedicels; pl. 62(1–7).

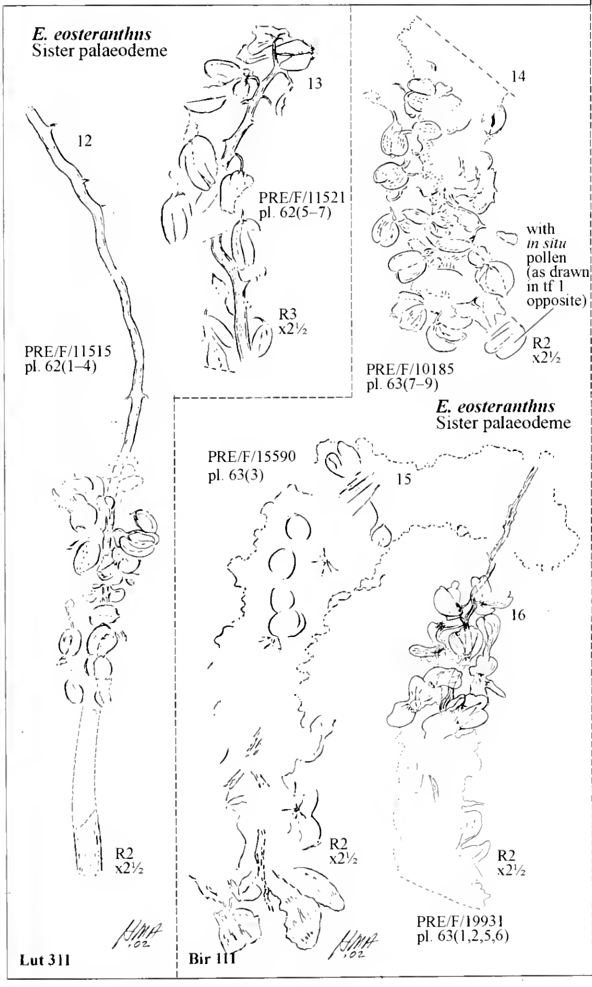
Specific diagnosis
An *Eosteria* species with a linear, gracile strobilus and microsporangial sacs dehiscing into two strongly unequal groups of three lobes.

Specific characteristics
Strobilus: linear, gracile (to *ca* 40 mm).
Microsporangium: cupulate sacs dehiscing into two unequal groups of 3 lobes, with a wide angle between the upper and lower sets of lobes, outer pair of proximal lobes with distinctive rib.

Etymology
eosteranthus—a male cone from the Easter Egg Shale (i.e. Aas 311).

Comment & comparison
E. eosteranthus is distinguished from *E. telemanthus* in the more gracile form of the strobilus and the clearer separation into distal and proximal lobes in the opened microsporangium. The specimens from Bir 111 and Lut 311 are included in this species, but with better preserved material they may well prove to be distinct.





Ginkgoites Seward 1919

Type species
Ginkgoites obovata Seward 1919.
Bjuv, Scania, Sweden; Rhaetic, Triassic.

Generic concept

A ginkgoopsid leaf with distinct long petiole, deeply dichotomously dividing fan-shaped lamina, and radiating, repeatedly forking subparallel venation.

Generic characters (Molteno Fm.)

Attachment: unknown.

Leaf: fan-shaped with margins diverging at >90°, lamina deeply dichotomously divided into several segments, with each segment variously lobed; petiole distinct, long, gracile; veins radiating from base, repeatedly forking, close to well spaced, running subparallel to terminate at distal margin.

Cuticle: see And. & And. (1989, p. 220); this vol., tfs 1–4 below.

Etymology

Ginkgoites—referring to similarity to *Ginkgo*.

Global range: numerous spp., Pangaea, ?Tr.–Tertiary.

Gondwana Triassic occurrence

Frequency (F): 21 degree squares (of the 84 across Gondwana).
Ubiquity (U): 4 continents (of 5 comprising Gondwana).
Diversity (D): 9 foliage species.
Abundance (A): <1% (the norm in Molteno TCs).
Longevity (L): 17 myrs (Spathian to early Carnian).

Colonisation success: FUDAL rating 21/4/9/–/17 = 51.
Intermediate success (Grade 3): *Ginkgoites* was the 7th most prominent genus in the Gondwana Triassic; it was relatively frequent, ubiquitous, diverse and long-lived, but markedly lacking in abundance.

Endemism: of the 9 species, 6 are single-assemblage endemics, 1 is a basin endemic, 1 a continent endemic, while the last is particularly widespread and variable and occurs throughout the realm.

Molteno occurrence

Frequency (F): 19 TCs (of 100 sampled in the Molteno).
Diversity (D): 6 species.
Abundance (A): occasional to common (1–5%) in 5 TCs; rare to very rare (<1%) in 14 TCs.

Habit: probably a tall deciduous tree.
Preferred habitat: a scattered element in riparian forest and woodland.

Affiliated organs

Female strobilus: *Avatia*—Grade 2 (Kin. reinf., Mut. occ.).
Male strobilus: *Eosteria*—Grade 3 (Kin. reinf., Mut. occ.).

Classification & comparison

The generic names *Ginkgo* and *Ginkgoites* are both in common use for fossils (see Stewart & Rothwell 1993, p. 390). In And. & And. (1989, p. 218), we followed Harris & Millington (1974) and used *Ginkgo*. However, in the absence of fruit allied to the extant *Ginkgo*, it seems more appropriate to name the Molteno fossils *Ginkgoites*.

Intergeneric comparison

Gondwana Triassic—In the dichotomising nature of both lamina and venation, *Ginkgoites* and *Sphenobaiera* are clearly the most alike of the ginkgoopsid leaf genera. In epidermal structure, however, *Ginkgoites* is also similar to *Sphenobaiera*, *Lepidopteris* and *Dejerseya*, but can be distinguished by the finer details of the cuticles. The cuticles of all three species of *Ginkgoites* occurring at Lit 111 (Tab. 46) are illustrated and described in And. & And. (1989).

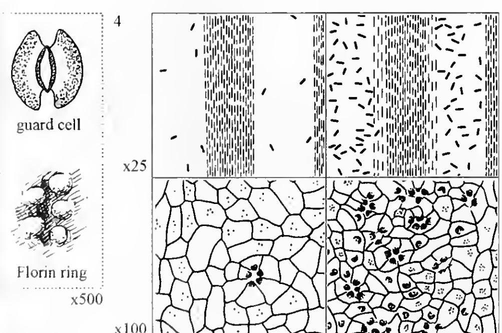
The leaf species that in gross morphology is closest to the extant *Ginkgo biloba* has here been transferred to the new genus *Paraginkgo* (p. 208). The cuticular details of this species, *P. antarctica*, are markedly distinct from both the extant *Ginkgo biloba* and fossil *Ginkgoites* cuticles.

Interspecific comparison

The nine species of *Ginkgoites* recognised from the Gondwana Triassic fall readily within the compass of the genus. The cuticle, however, is known for only three of these species, so confirmation is not at hand from this valuable source. The six Molteno *Ginkgoites* species are based on distinct, nonoverlapping reference palaeodemes. While most species, as known, are single-assemblage endemics, one species (*G. matatiensis*) is highly polymorphic and occurs in 16 Molteno TCs.

Ginkgoites matatiensis
Lit 111 PRE/F/5485

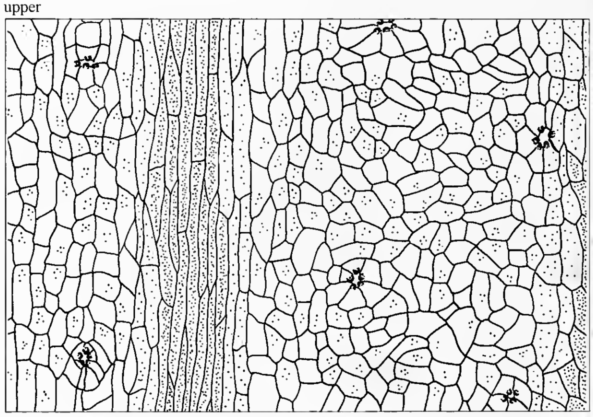
4 3



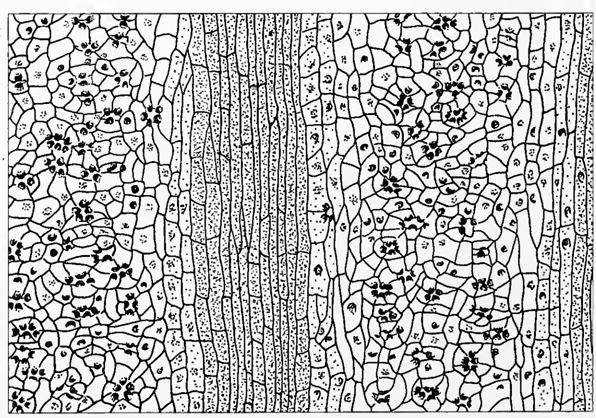
tfs 1–4 from And. & And., 1989

upper

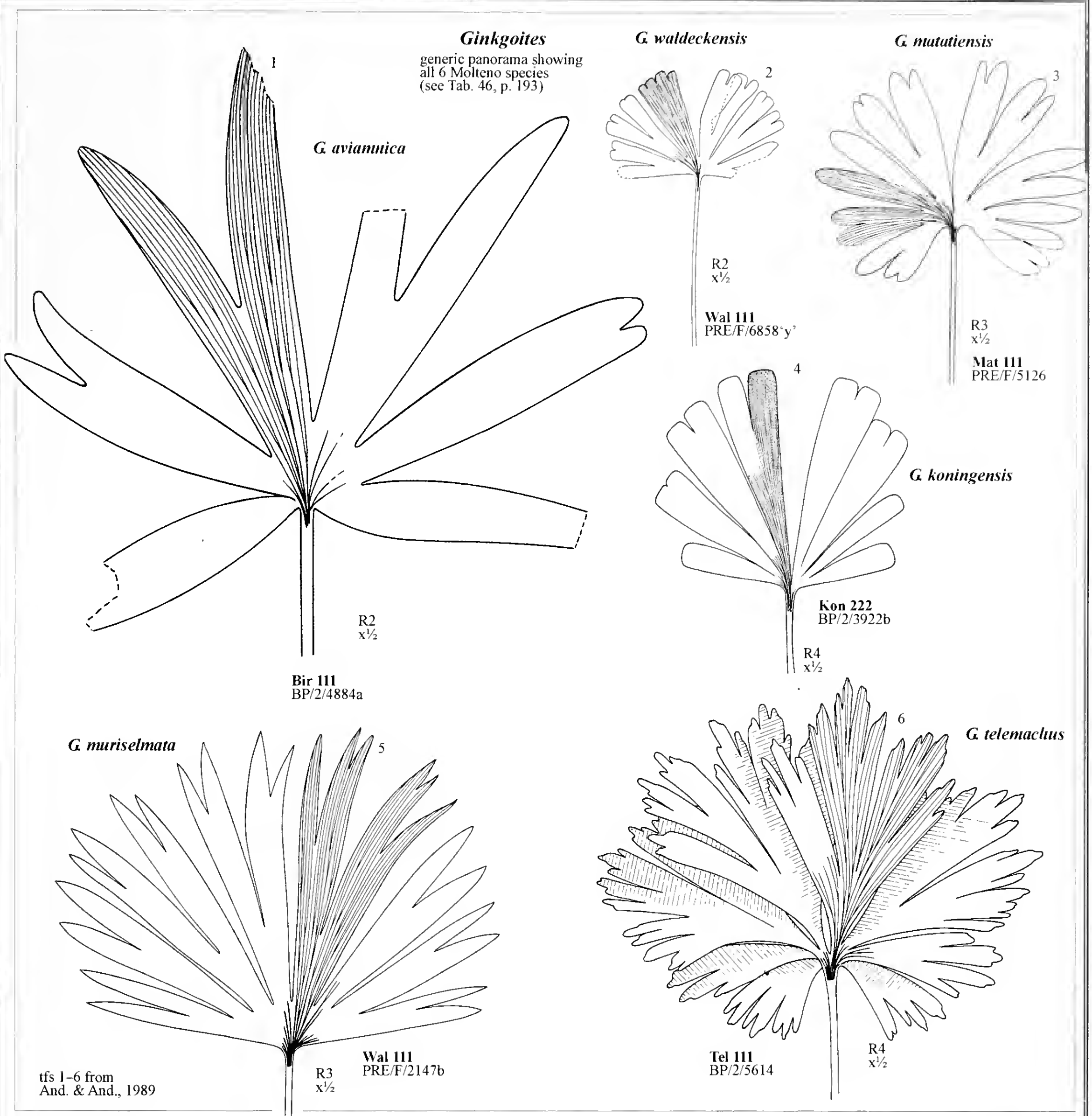
1

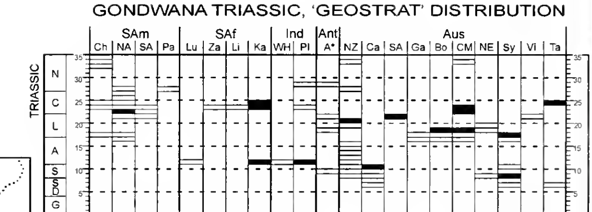


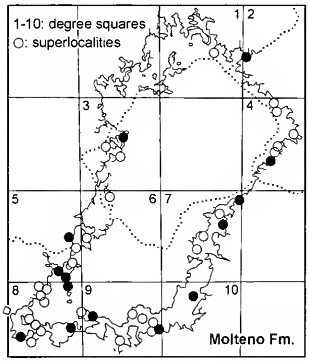
2

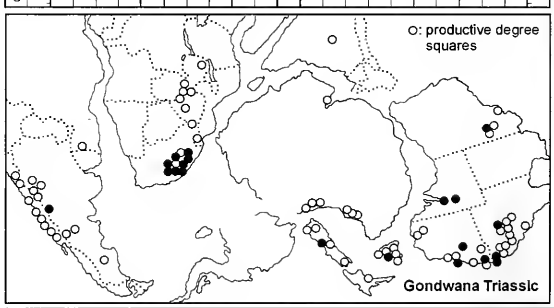


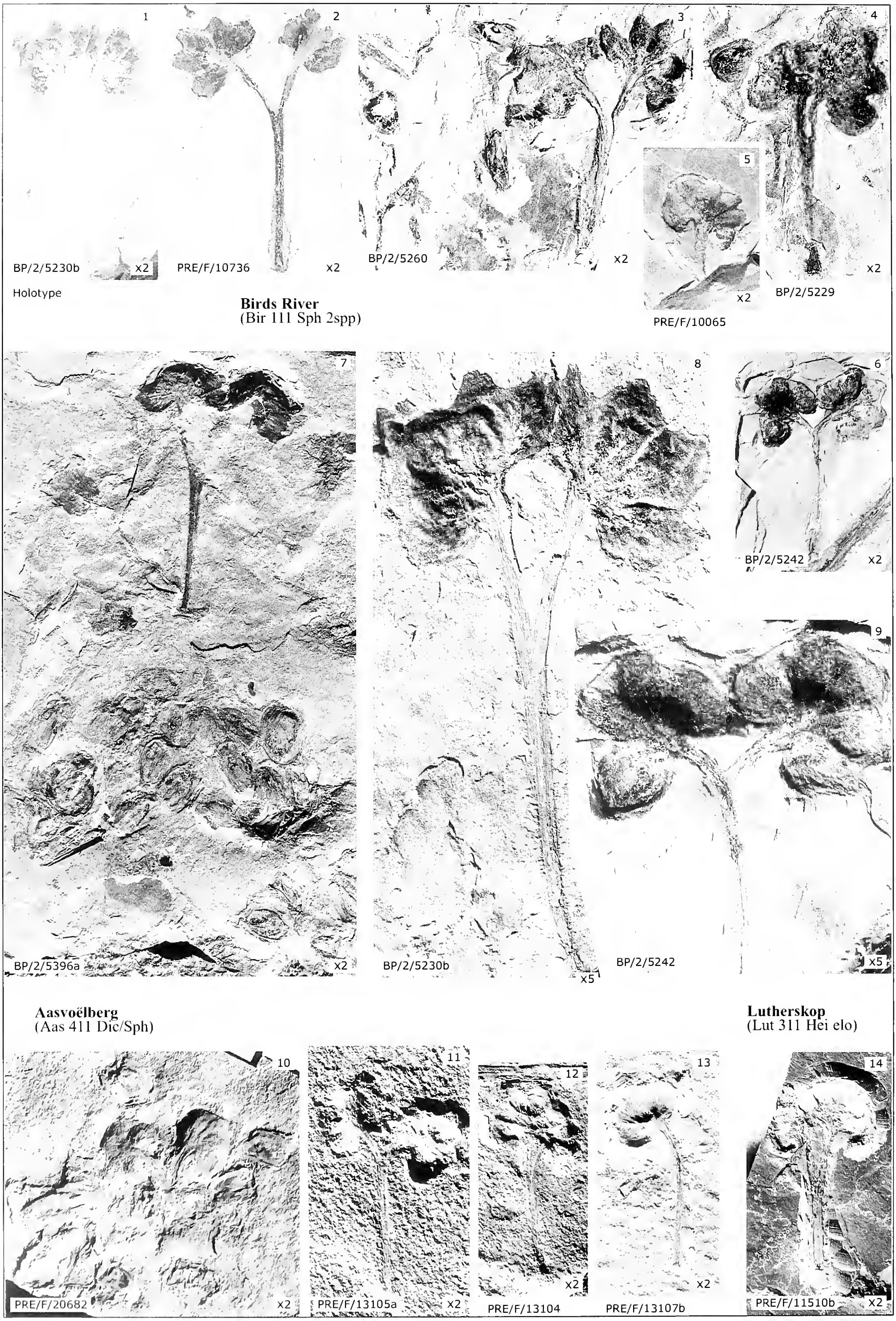
lower x100

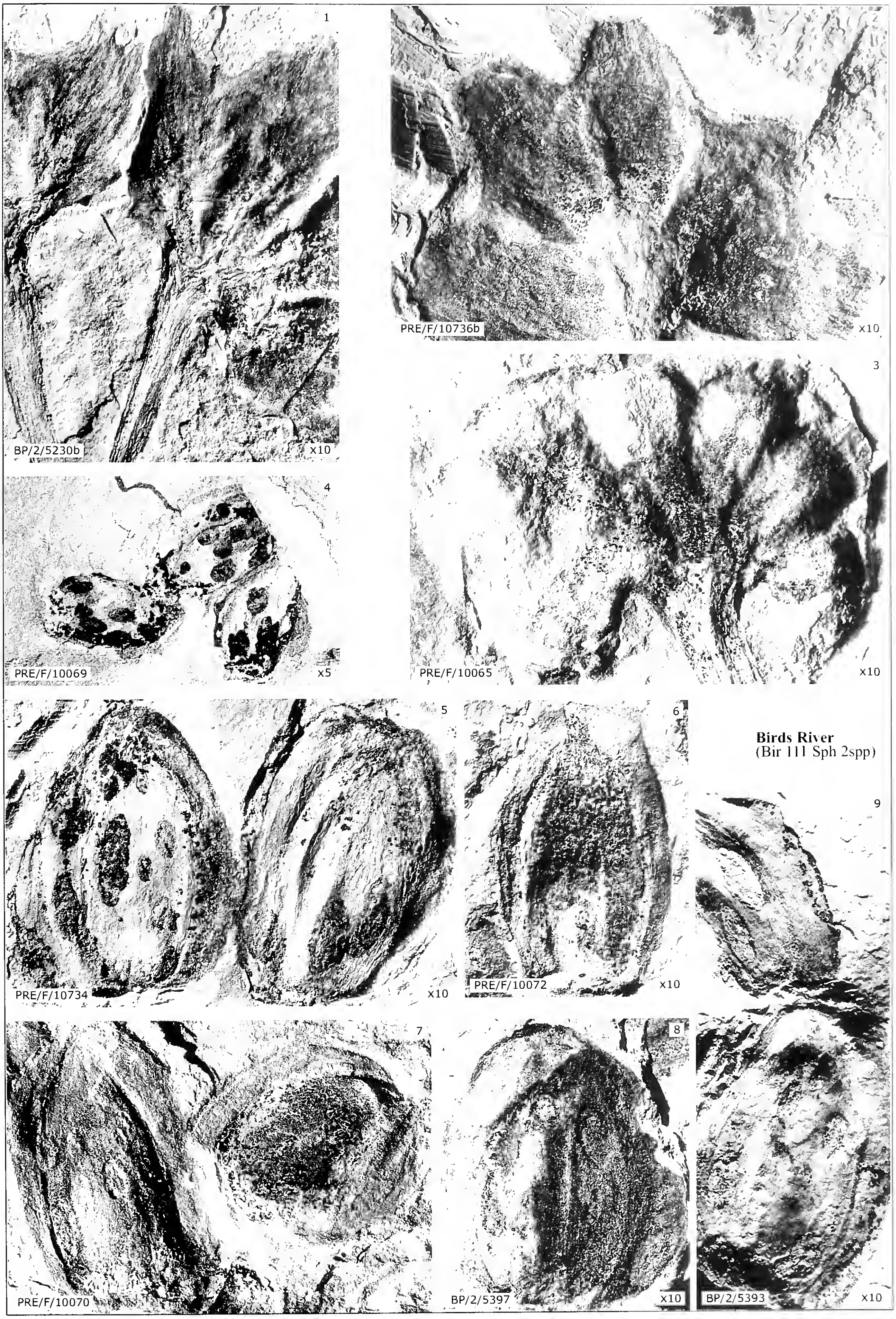

Ginkgoites
generic panorama showing all 6 Molteno species (see Tab. 46, p. 193)
1
G. aviannica
R2
x½
Bir 111
BP/2/4884a
G. waldeckensis
2
R2
x½
Wal 111
PRE/F/6858'y'
G. matatiensis
3
R3
x½
Mat 111
PRE/F/5126
4
G. koningensis
Kon 222
BP/2/3922b
R4
x½
G. muriselmata
5
tfs 1–6 from
And. & And., 1989
R3
x½
Wal 111
PRE/F/2147b
6
G. telemachus
Tel 111
BP/2/5614
R4
x½


GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION
SAm
SAf
Ind
Ant
Aus
Ch
NA
SA
Pa
Lu
Za
Li
Ka
WH
Pl
A*
NZ
Ca
SA
Ga
Bo
CM
NE
Sy
Vi
Ta
TRIASSIC
N
C
L
A
S
G

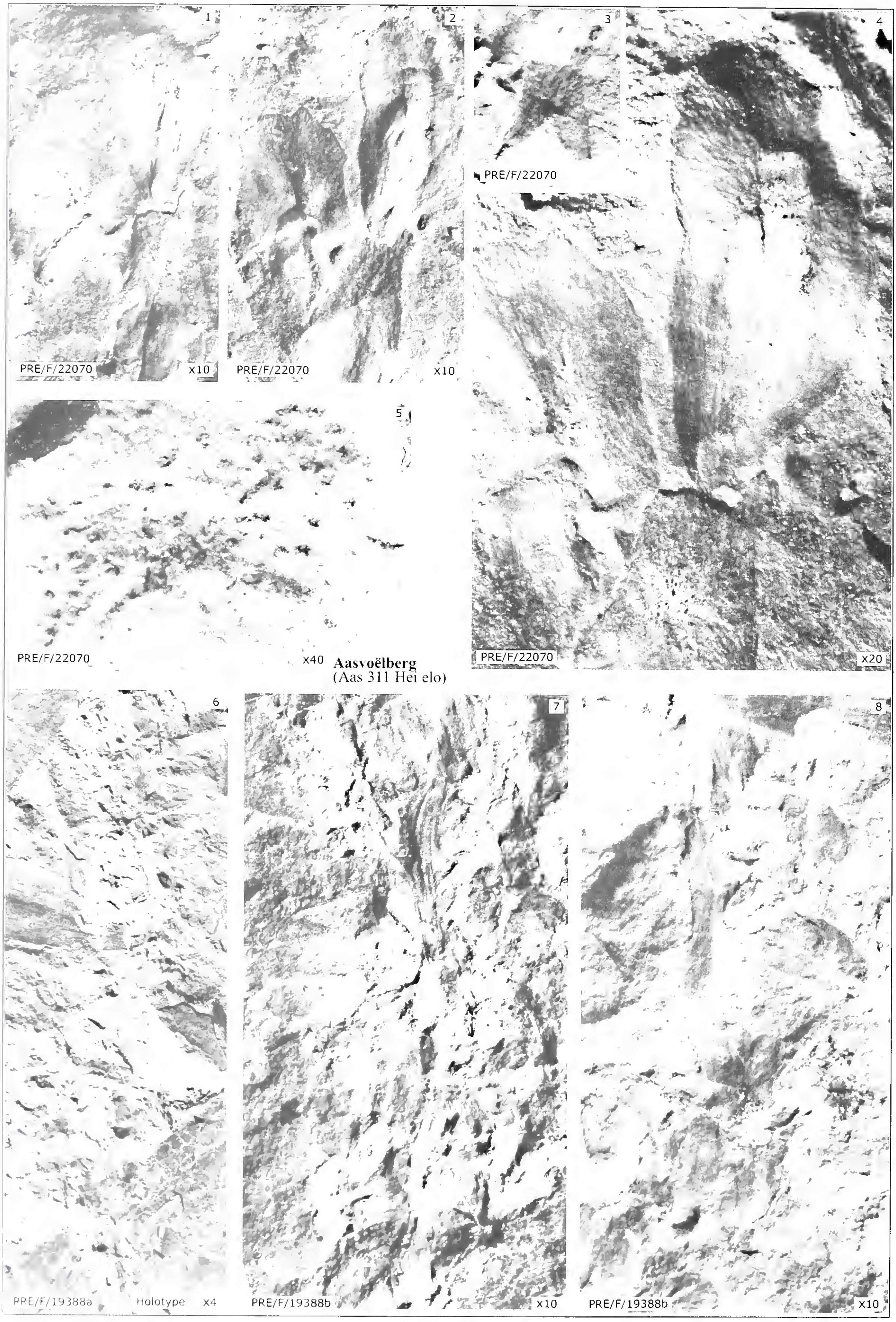

1-10: degree squares
○: superlocalities
Molteno Fm.


○: productive degree squares
Gondwana Triassic

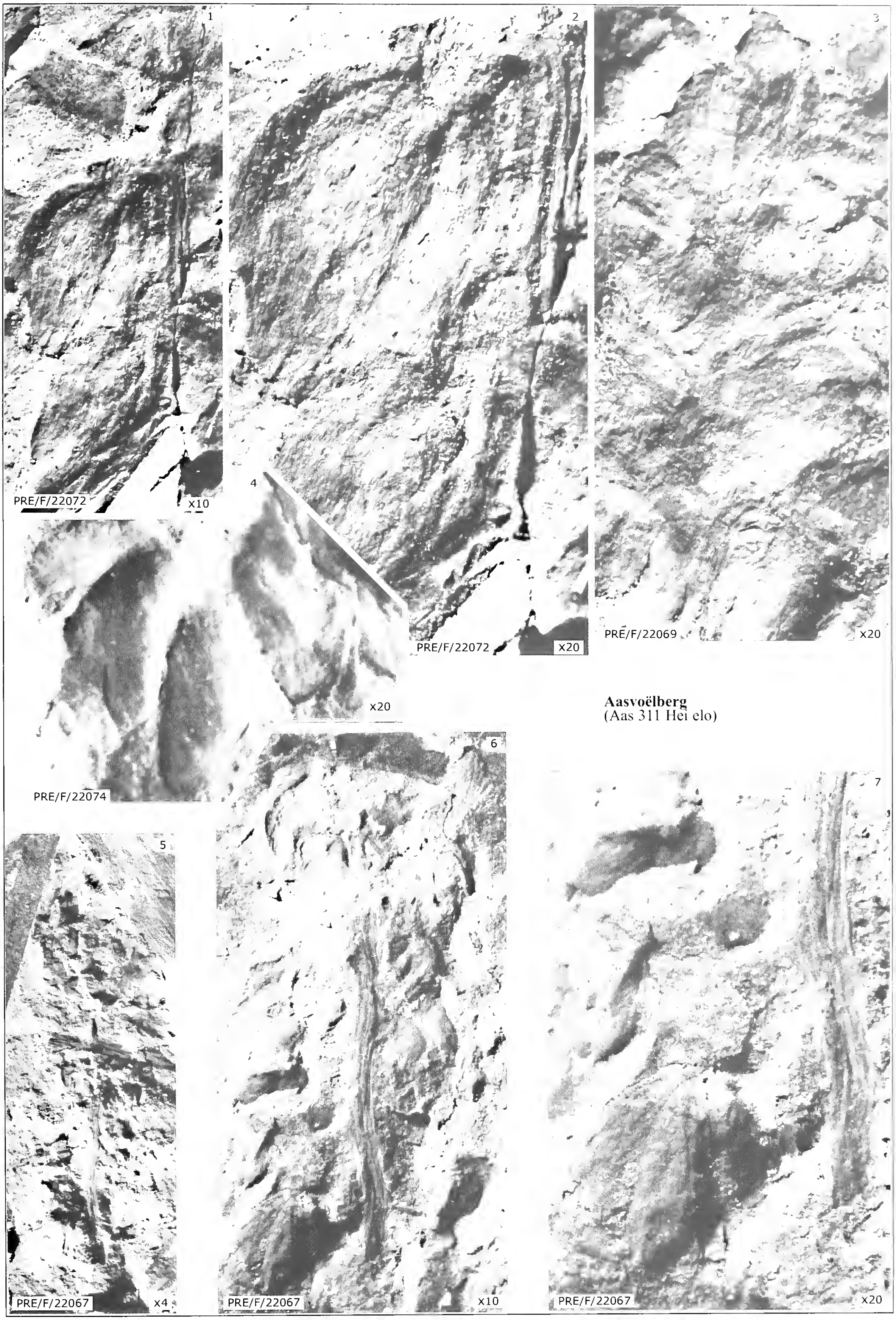

1
2
3
4
5
BP/2/5230b
x2
Holotype
PRE/F/10736
x2
BP/2/5260
x2
x2
PRE/F/10065
x2
BP/2/5229
Birds River
(Bir 111 Sph 2spp)
7
8
6
BP/2/5242
x2
9
BP/2/5396a
x2
BP/2/5230b
x5
BP/2/5242
x5
Aasvoëlberg
(Aas 411 Dic/Sph)
Lutherskop
(Lut 311 Hei elo)
10
11
12
13
14
PRE/F/20682
x2
PRE/F/13105a
x2
x2
PRE/F/13104
x2
PRE/F/13107b
PRE/F/11510b
x2

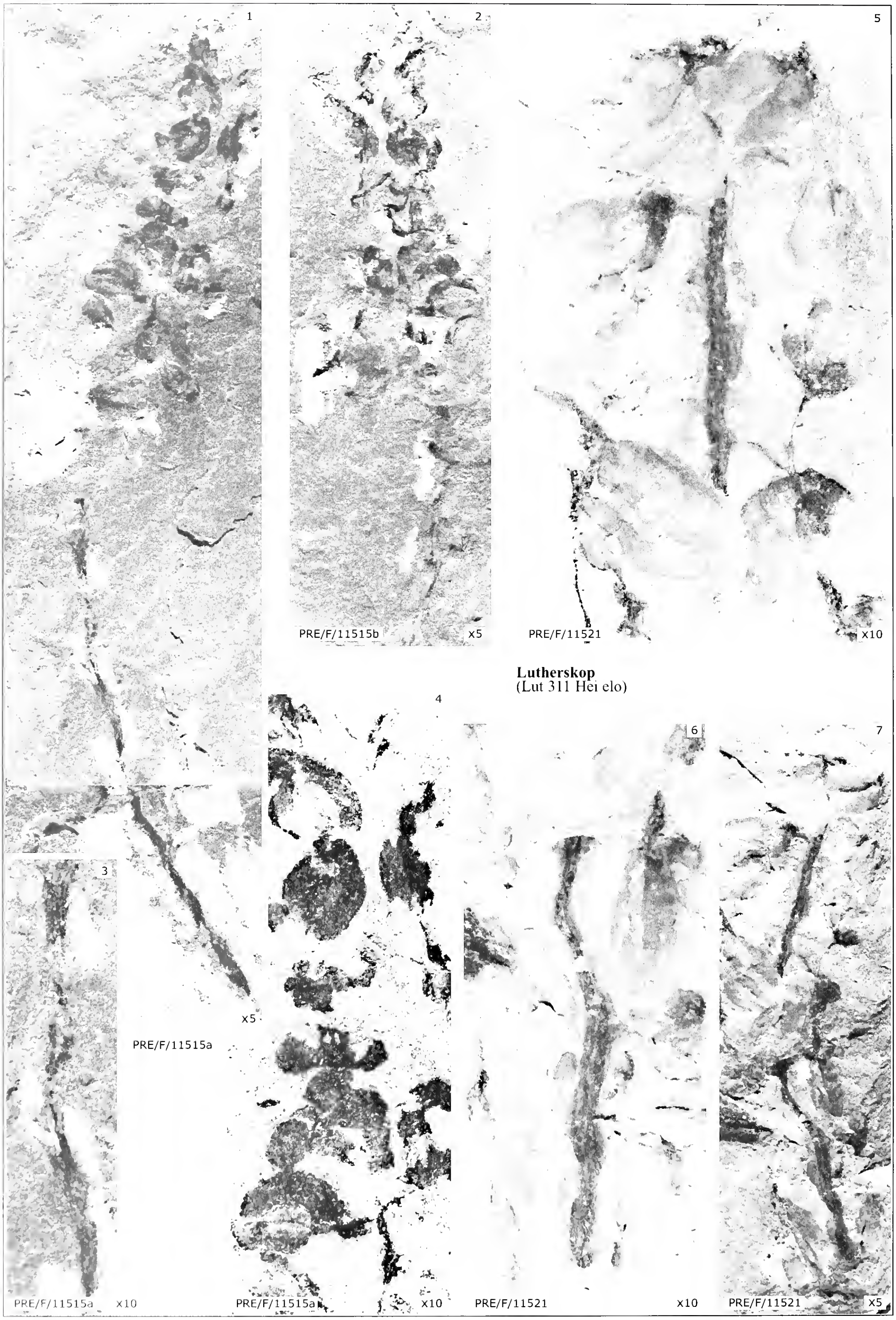


GINKGOALES **pl. 59** *Avatia bifurcata*

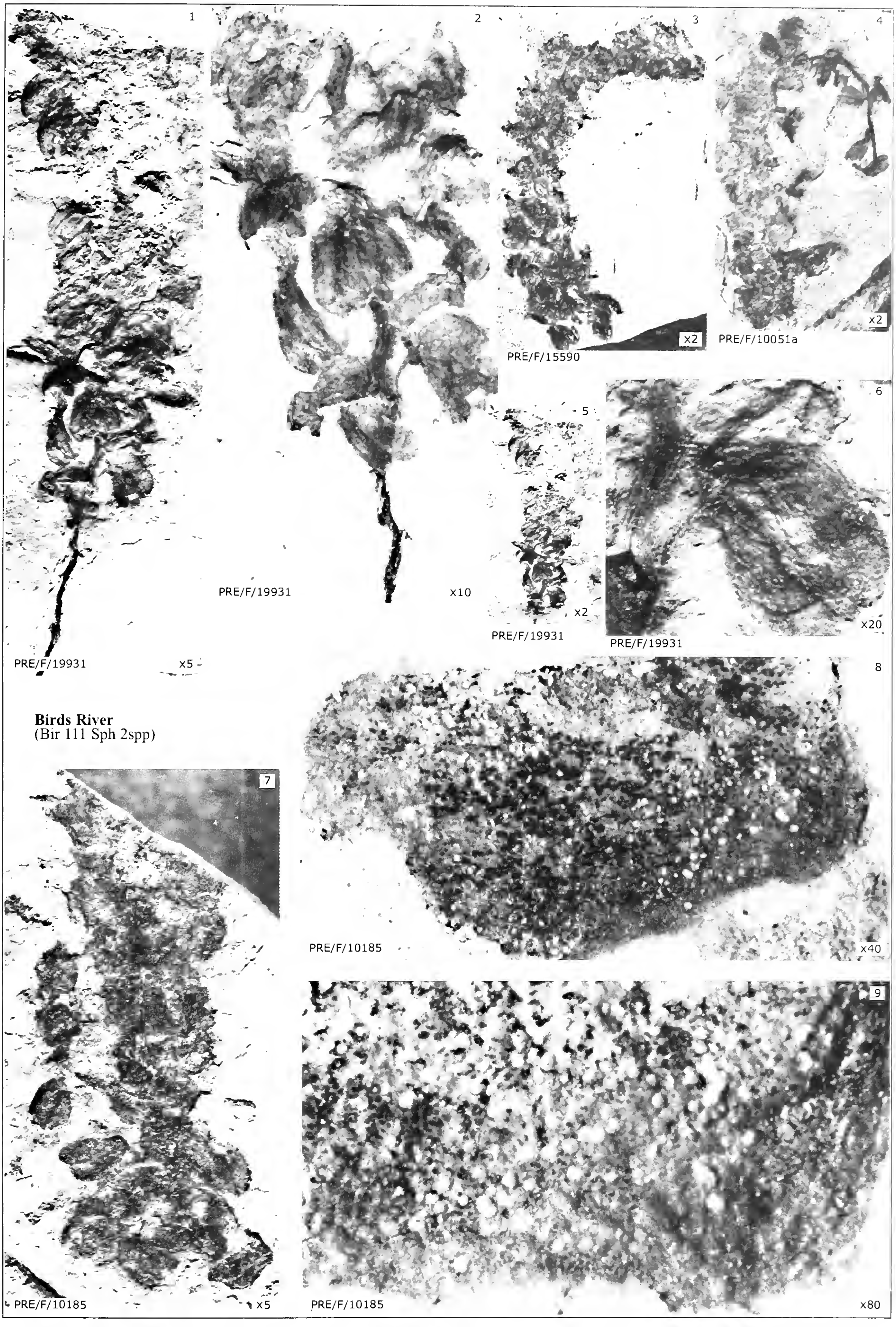


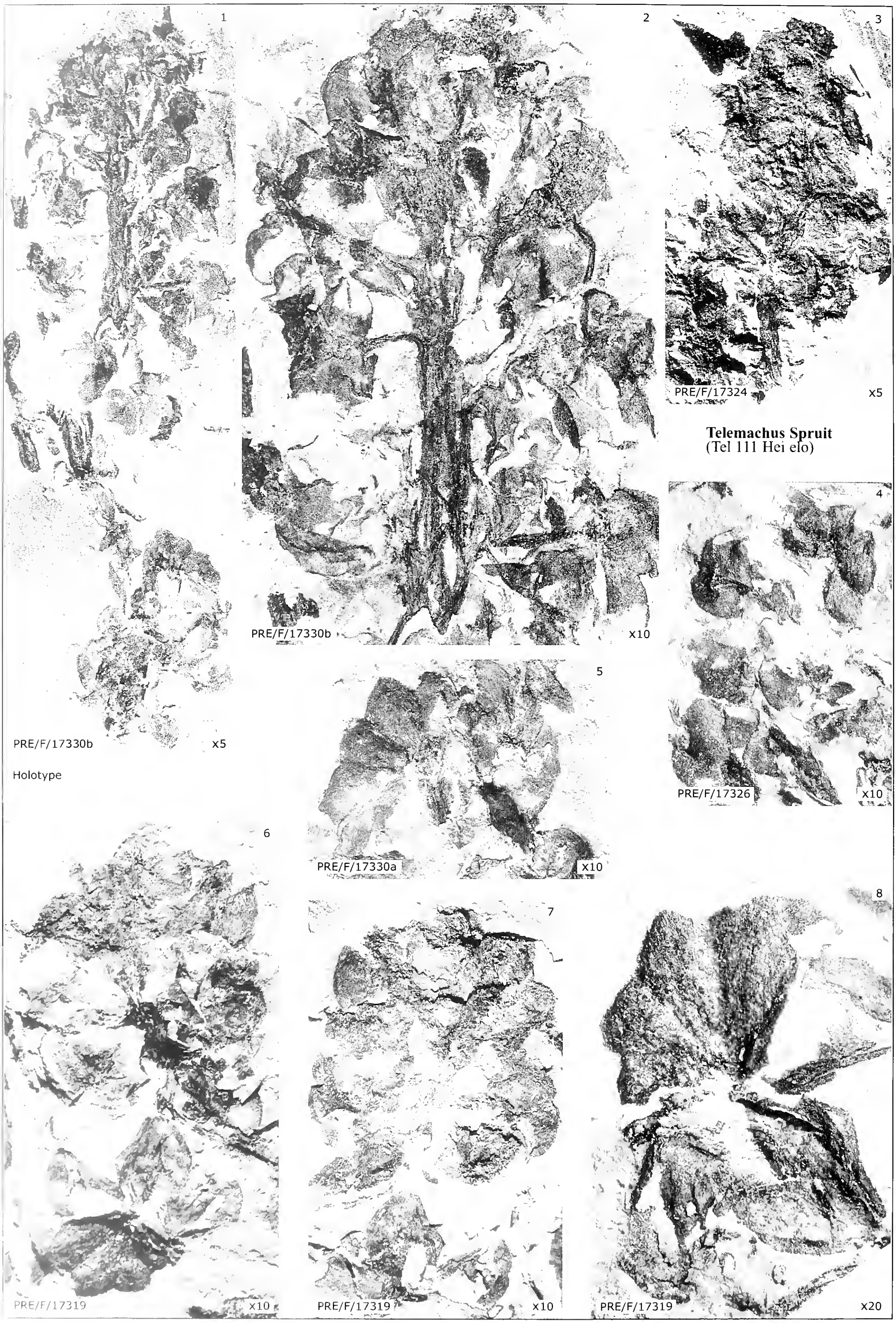
Eosteria eosteranthus **pl. 60** **GINKGOALES**


1
PRE/F/22072
x10
2
PRE/F/22072
x20
3
PRE/F/22069
x20
4
x20
PRE/F/22074
Aasvoëlberg
(Aas 311 Hei elo)
5
PRE/F/22067
x4
6
PRE/F/22067
x10
7
PRE/F/22067
x20

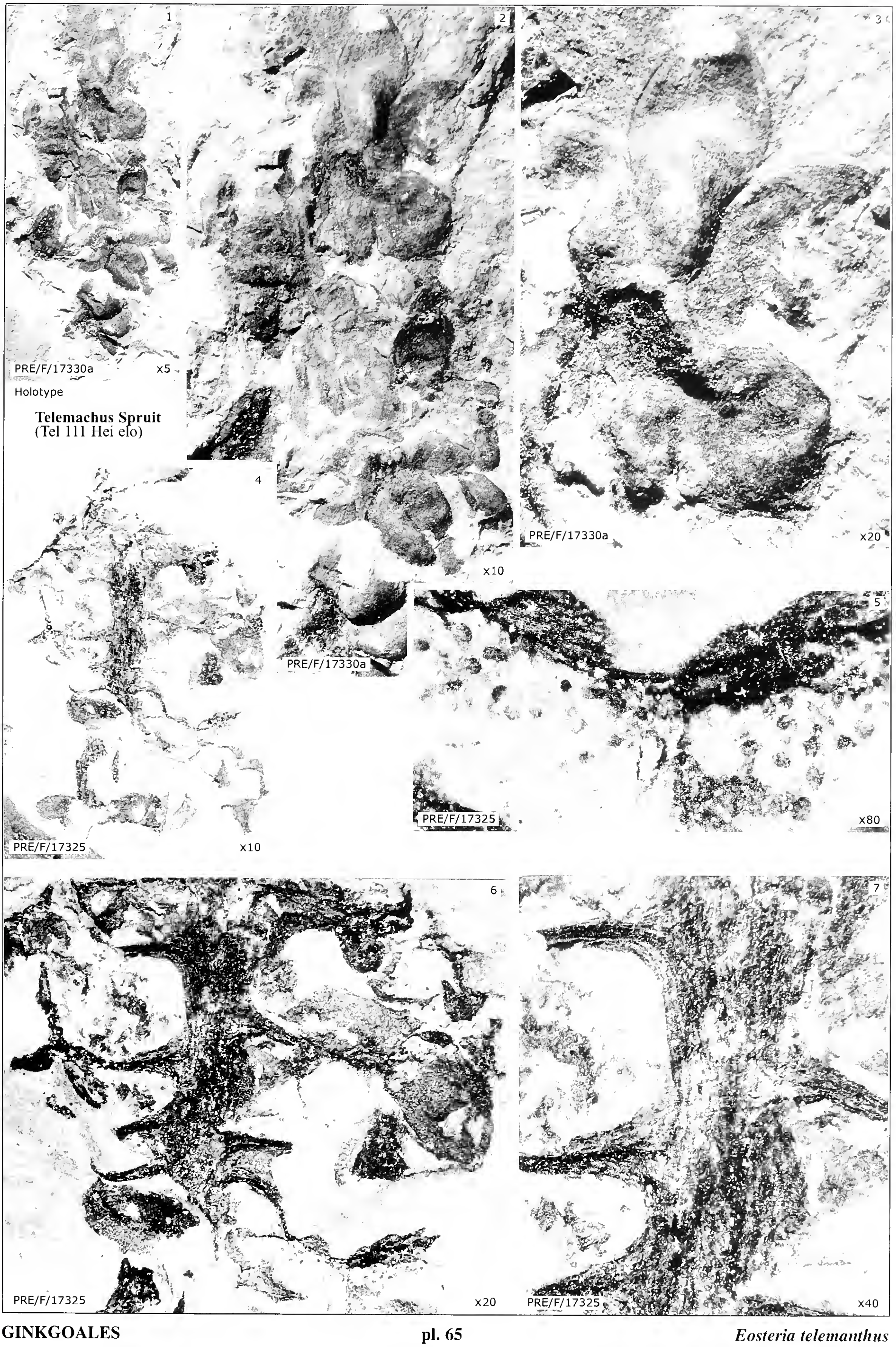


Eosteria eosteranthus **pl. 62** **GINKGOALES**


1
PRE/F/19931
x5
2
PRE/F/19931
x10
3
x2
PRE/F/15590
4
x2
PRE/F/10051a
5
x2
PRE/F/19931
6
x20
PRE/F/19931
Birds River
(Bir 111 Sph 2spp)
7
PRE/F/10185
x5
8
PRE/F/10185
x40
9
PRE/F/10185
x80



Eosteria telemanthus **pl. 64** **GINKGOALES**


1
PRE/F/17330a x5
Holotype
Telemachus Spruit
(Tel 111 Hei elo)
2
PRE/F/17330a x10
3
PRE/F/17330a x20
4
PRE/F/17325 x10
5
PRE/F/17325 x80
6
PRE/F/17325 x20
7
PRE/F/17325 x40

GINKGOOPSIDA S.V.Meyen 1984
GINKGOALES Engl. 1897
INCERTAE SEDIS family

Paraginkgo J.M.And. & H.M.And., gen. nov.

Type species
Salisburia antarctica Saporta 1882.
Sydney Basin, Australia; Ladinian, Triassic.

Generic diagnosis
A ginkgoopsid leaf with short gracile petiole, entire fan-shaped lamina and radiating, forking, closely spaced, subparallel venation and distinct cuticle.

Generic characters (Molteno Fm.)
Attachment: unknown.
Leaf: small (*ca* 30 x 60 mm), broadly fan-shaped with margins diverging at >90°, lamina entire to sinuate with occasional shallow clefts; petiole distinct, short, gracile; veins radiating from base, repeatedly forking, closely spaced and subparallel (20 per 10 mm at distal margin).
Cuticle: see And. & And. (1989, p. 220); this vol., tfs 1–4 opposite.

Etymology
Paraginkgo—with reference to the similarity in gross form to extant *Ginkgo biloba* leaves.

Global Range: 1 sp., Gondwana, U.Tr. (LAD–CRN).
First: *Paraginkgo antarctica* (And. & And. 1989, p. 540); Culvida Sdst., Mt Ernest (C62), Canning Basin, Western Australia.
Last: the Molteno species described here.

Gondwana Triassic occurrence (after And. & And. 1989)
Frequency (F): 5 degree squares (of the 84 across Gondwana).
Ubiquity (U): 2 continents (of 5 comprising Gondwana).
Diversity (D): 1 foliage species.
Abundance (A): <1% (the norm in Molteno TCs).
Longevity (L): 14 myrs (Spathian–Carnian).

Colonisation success: FUDAL rating 5/2/1/–/14 = 22.
Limited success (Grade 2): *Paraginkgo* was the 16th most prominent genus in the Gondwana Triassic; it was widespread (though disjunct) and long-lived, but lacking in frequency, abundance and diversity.
Endemism: the single species had a disjunct distribution (Karoo Basin and Australia).

Molteno occurrence
Frequency (F): 2 TCs (of 100 sampled in the Molteno).
Diversity (D): 1 species.
Abundance (A): very rare (<1%) in both TCs.

Habit: probably a shrub.
Preferred habitat: *Dicroidium* riparian forest.

Affiliated organs: unknown.

Classification & comparison
The systematic position of *P. antarctica* is problematic. In gross form it closely resembles the extant *Ginkgo biloba*. However, the cuticle of this extant species does not appear to be closely related to either the fossil *Ginkgoites* species or to *P. antarctica*. The cuticle of *P. antarctica* is distinctly different from that of *G. matatiensis* and *G. telemachus* from Lit 111 which have lappetate subsidiary cells and no striae on the guard cells. Nor does it resemble the cuticle of the bulk of other fossil *Ginkgoites* species from around the globe. These latter form an apparently natural group to which *G. matatiensis* and *G. telemachus* belong.

Paraginkgo antarctica (Saporta) J.M.And. & H.M.And., comb nov.

Holotype
Specimen: catalogue number and repository not in literature. See Saporta [1882, tf. 1(1)] and And. & And. [1989, pl. 320(1)].
Assemblage/locality: Sydney region, Wianamatta Grp., Sydney Basin, Ladinian, Triassic.

Reference assemblage & palaeodeme
Assemblage: Lit 111 Dic/Hei, Little Switzerland.
Specimens: 40 individuals (see And. & And. 1989, pl. 113–118).
Cuticle: well preserved.

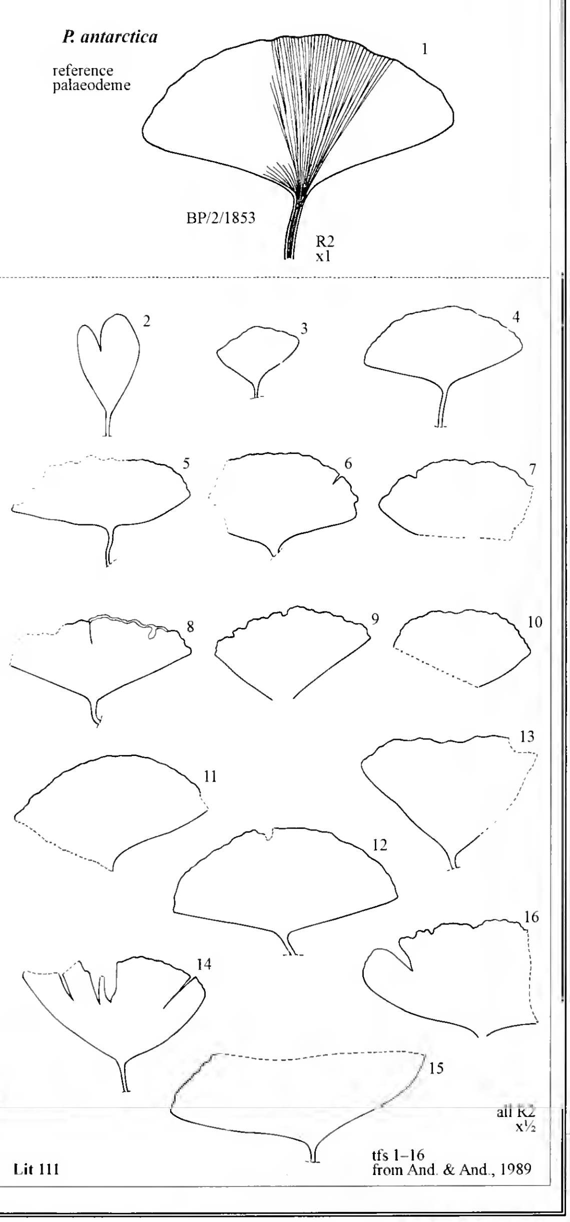
Sister palaeodeme
San 111 Dic cra: 3 indivs.

Specific diagnosis: as for genus.

Specific characters: as for genus.

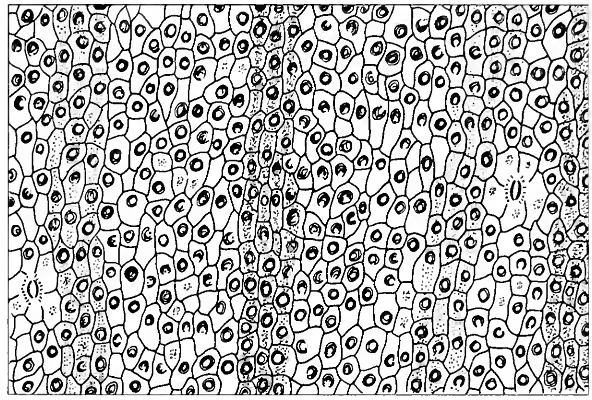
Etymology
antarctica—probably for the southern occurrence of the species.

Comment & comparison: as for genus.

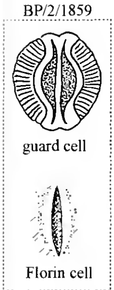


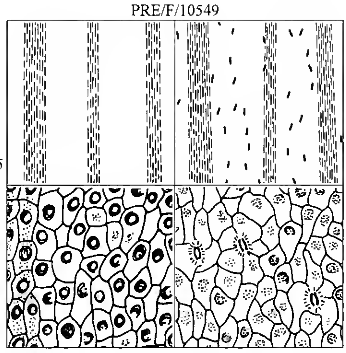
Cuticles

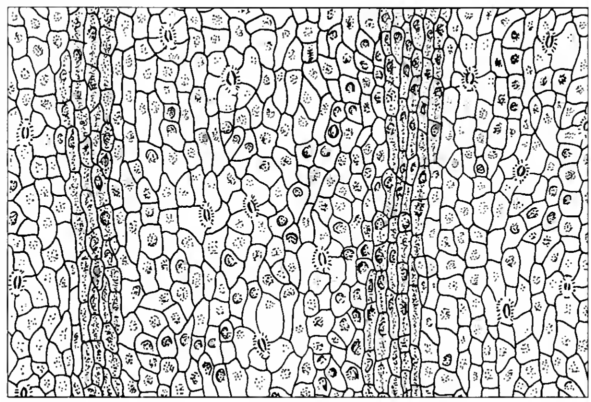
Potential sample: Lit 111, 40 indivs.
Macerated (this work): Lit 111, 3 indivs.
Preservation grade: Grade 5.
Diagnostic characters: with nonlappetate subsidiary cells and guard cells with strong radial striae.
Comment: *Paraginkgo* has been separated from *Ginkgoites* primarily on the basis of its very distinctive cuticle.
Significance:
Classification—of no aid beyond suggesting the class Ginkgoopsida.
Affiliations—no foliage species with known cuticle matches this.



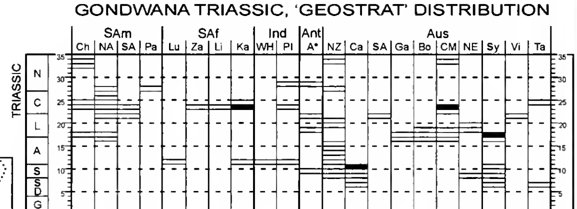
P. antarctica

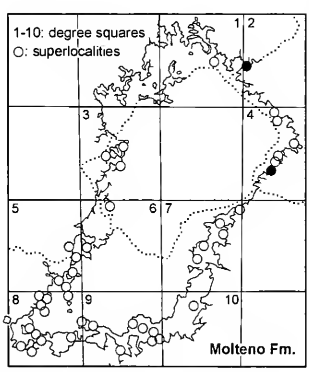


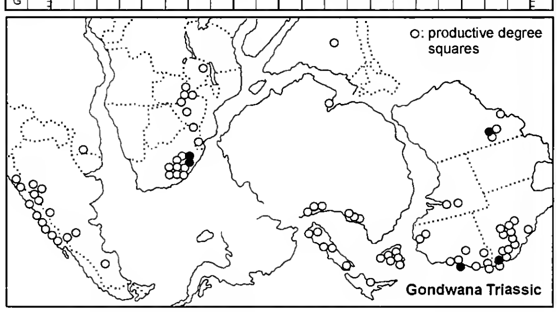




tfs 1–4
from And. & And., 1989







GINKGOOPSIDA S.V.Meyen 1984
HAMSHAWVIALES J.M.And. & H.M.And., ord. nov.
HAMSHAWVIACEAE J.M.And. & H.M.And., fam. nov.

Hamshawvia J.M.And. & H.M.And., gen. nov.

Type species
Hamshawvia baccata J.M.And. & H.M.And., sp. nov.
Umkomaas Valley, Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis
A ginkgoopsid strobilus consisting of a simple, once-forked axis, bearing a pair of megasporophylls each consisting of single, erect, fleshy, rounded multiovulate lamina.

Generic characters (based on the 4 Molteno species)
Attachment: Strobili borne on a short shoot with several *Sphenobaiera* leaves.
Strobilus: simple, lax, bilaterally symmetrical, small (*ca* 15–40 mm long); axis relatively gracile, short to elongate, distally forked; megasporophylls a single distal pair.
Megasporophyll: simple, pedunculate; ovuliferous lamina rounded to cordiform, apparently fleshy, bilaterally symmetrical, flattened dorsiventrally, sometimes apparently longitudinally folded; ovules/seeds adaxial, embedded, *ca* 8–20 in number, arranged radially to semiradially or bilaterally on either side of a median vein or receptacle.
Ovule/seed: small (up to *ca* 1 mm long), generally elliptical; with a slightly elongate central marking (?embryo).

Eponymy
Hamshawvia—in honour of Hugh Hamshaw Thomas, one of the pioneer collectors from the famous Umkomaas Valley (Umk 111) locality.

Global range: 5 spp., Gondwana Tr. (ANS–CRN).
First: *Hamshawvia* sp. (Holmes 1995); Basin Creek Fm., Nymboida, N.S.W., Australia.
Last: the 4 Molteno species described here.

Gondwana Triassic occurrence
SAm—Argentina, 1 TC (1 indiv.).
SAf—Karoo Basin, 4 TCs (24 indivs).
Aus—Nymboida Sub-basin, 1 TC (2 indivs).

Molteno occurrence
Frequency (F): 4 TCs (of 100 sampled in the Molteno).
Diversity (D): 4 species.
Abundance (A): 24 indivs total, very rare to extremely rare.

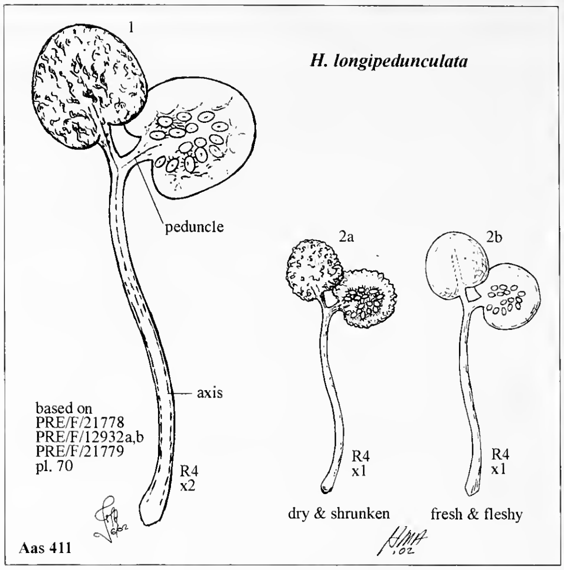
Aas 411 Dic/Sph:	14 indivs	in 512	man-hrs	(1 per	4	man-days)	very rare	
Lut 311 Hei elo:	1 "	" 50	"	(1 "	5	")	"	
Umk 111 Dic 2spp:	7 "	" 400	"	(1 "	6	")	extremely rare	
Lit 111 Dic/Hei:	2 "	" 550	"	(1 "	27	")	"	"

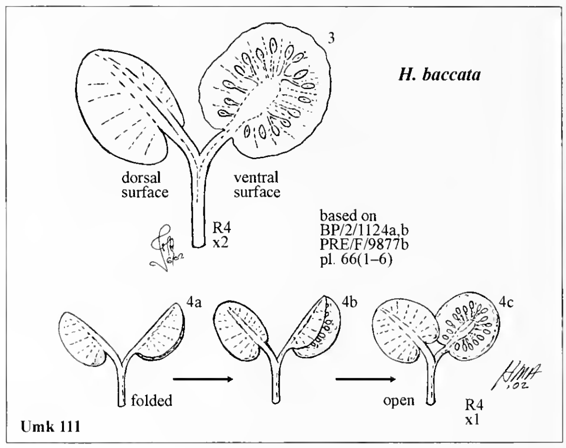
Hamshawvia is an infrequent and very rare element in the Molteno.

Affiliated organs (for details see p. 213)
Male strobilus: *Stachyopitys*—Grade 4 (Mut. occ., Kin. reinf.).
Foliage: *Sphenobaiera*—Grade 4/5 (Mut. occ., Kin. reinf., Org. att., Cut. corr.).

Classification & comparison
Suprageneric classification (Hamshawviaceae/Hamshawviales)
Without considering the supposed affiliated organs of *Hamshawvia*, it would be particularly difficult to classify this genus. The simple forked strobilus and the cuticle suggest the Ginkgoopsida, while the multiovulate heads (megasporophylls) hint more towards the Bennettitopsida. However, with the *Sphenobaiera* and *Stachyopitys* affiliation taken into consideration, placement within the Ginkgoopsida—close to *Dicroidium* (Umkomasiaceae) and *Ginkgoites* (Avatiaceae)—is favoured. The differences between *Hamshawvia* and any of the other ovulate Gondwana-Triassic ginkgoopsid genera are profound enough to erect a new order (Hamshawviales) and family (Hamshawviaceae) for this plant-genus.

Intergeneric comparison (Gondwana Triassic)
Of the ginkgoopsid ovulate genera in the southern Triassic kingdom, *Avatia* is perhaps the nearest to *Hamshawvia*. Both genera consist of simple once-forked strobili attached, most likely, in the same manner as in the extant *Ginkgo biloba*, to short shoots. *Avatia* differs in its leafy 4- or 5-lobed heads and its readily dehisced winged seeds.

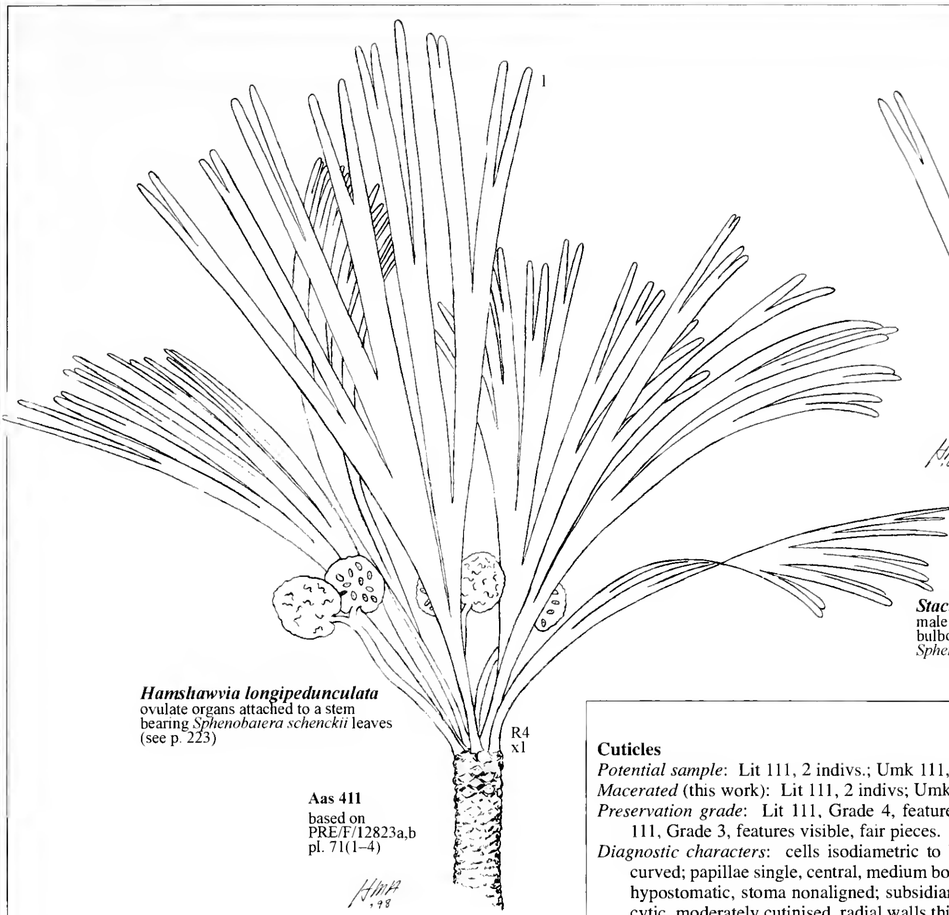


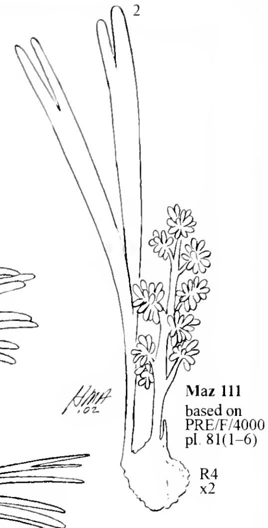


Reconstructions
Hamshawvia longipedunculata (Aas 411)
The R4 reconstruction is based on three specimens in particular: PRE/F/12932b (p. 215, tf. 2) for the forked pair of megasporophylls; PRE/F/21778 (p. 215, tf. 1) for the arrangement of seeds in the apparently fleshy megasporophyll head; and PRE/F/21779 (p. 215, tf. 4) for the elongate peduncle.
A characteristic feature seen in a few specimens, most clearly in PRE/F/21438 (p. 215, tf. 5), is the radiating pattern developed around each seed. This feature is interpreted as the result of postmaturity shrinkage. We suggest that in life the megasporophyll was a fleshy structure with embedded seeds, well adapted for dispersal by fructivores.

Hamshawvia baccata (Umk 111)
The R4 reconstruction is a combination of two specimens: PRE/F/1124 (p. 214, tf.1) for the overall form of the strobilus and for the arrangement of seeds embedded within the inner face of the megasporophyll heads; and BP/2/9877b (p. 214, tf. 3) for the folding of the megasporophyll about a central rib.
In tfs 4a–c (above) our interpretation of the maturing megasporophylls as they unfold is shown. The mature heads were apparently flattened berry-like structures, but in the absence of shrinkage patterns, are seen as less fleshy than in *H. longipedunculata*.

Fertile short shoot (Aas 411)
The *Hamshawvia/Sphenobaiera* reconstruction (tf. 1 opposite) is based on PRE/F/12823a,b [pl. 71(1–4)], which bears a single (?)immature individual of *Hamshawvia* together with four *Sphenobaiera schenckii* leaves terminally on a (?)short shoot. In the reconstruction, we show three mature *H. longipedunculata* strobili within a cluster of several *S. schenckii* leaves as might have been expected in life.





Cuticles

Potential sample: Lit 111, 2 indivs.; Umk 111, 7 indivs.
Macerated (this work): Lit 111, 2 indivs; Umk 111, 2 indivs.
Preservation grade: Lit 111, Grade 4, features clear, good pieces; Umk 111, Grade 3, features visible, fair pieces.
Diagnostic characters: cells isodiametric to linear oblong, walls gently curved; papillae single, central, medium bold, restricted to one surface; hypostomatic, stoma nonaligned; subsidiary cells brachypara(actino)-cytic, moderately cutinised, radial walls thickened; guard cells elliptic; florin ring lappetate.
Comment: possible resin bodies noted adjacent.
Significance:

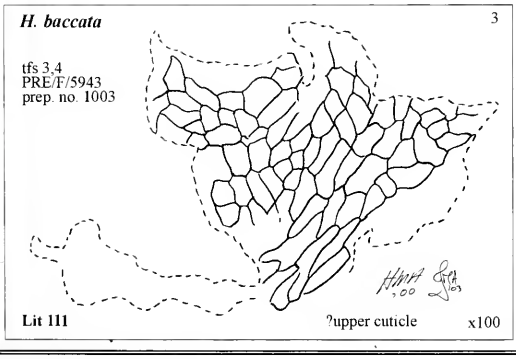
Classification—The cuticular features support the placement of *Hamshawvia* in the Ginkgoopsida which often have isodiametric, papillate cells, and lappetate subsidiary cells.

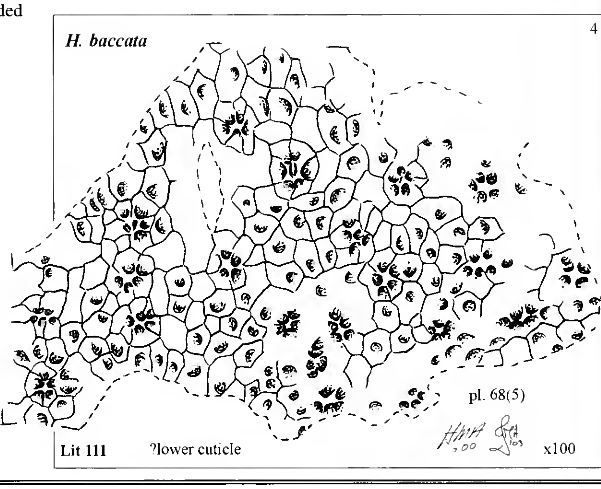
Affiliations—The *Hamshawvia* cuticle from Lit 111 is remarkably close to that of *Sphenobaiera schenckii* from the same TC (illustrated here under *Sphenobaiera* on p. 222 and previously described by And. & And. 1989, p. 142). This provides a particularly fine example of cuticular correspondence between female fruit and leaf.

Ovule/seeds

On the specimens available, the ovules/seeds are rarely seen or are barely evident. We assume that they were well embedded within the (?)fleshy fruit. The seeds are interpreted further as occurring in a single plane rather than radiating hemispherically from the median axis since some specimens from Umk 111, e.g. BP/2/9877b and BP/2/1125, show the folded nature of the head about the axis. However, this is not seen in the Aas 411 specimens which in the strongly wrinkled pattern indicate that the fruits were very fleshy and possibly more spherical. In PRE/F/21438a [pl. 70(7)], the ovules are particularly clear owing to the differential shrinkage of the surrounding tissue.

So far no ovules/seeds have been isolated by maceration. Specimen BP/2/1125, pl. 67(3–5), did yield ovoid opaque structures, but they are more likely to be resin bodies. Compare these with the more rounded (?)resin bodies from BP/2/1124, pl. 67(10, 11).





assemblages (taphocoenosis)		*Sphenobaiera*	♀ *Hamshawvia*	*H. baccata*	*H. longiped.*	*H. octosemina*	*H. linisemina*	*H. spp. indet*	Habitat
Umk 111	Dic 2spp	**5**	7	6	-	1	-	-	D1
Lit 111	Dic/Hei	**1**	2	2	-	-	-	-	
Hla 213	Dic elo	49	-	-	-	-	-	-	
" 212	Dic 3spp	7	-	-	-	-	-	-	
" 211	" "	7	-	-	-	-	-	-	
Maz 111	Dic cra	**12**	-	-	-	-	-	-	D2
" 211	Hei/Dic	**1**	-	-	-	-	-	-	
Mat 111	Dic dub	18	-	-	-	-	-	-	
Kap 111	Dic/Ris	20	-	-	-	-	-	-	
Cal 111	Dic/Sph	**44**	-	-	-	-	-	-	
Kom 111	Sph/Dic	**60**	-	-	-	-	-	-	
Vin 111	Dic odo	4	-	-	-	-	-	-	
Ela 111	" "	**1**	-	-	-	-	-	-	
Kra 111	" "	1	-	-	-	-	-	-	
Kon 223	" "	1	-	-	-	-	-	-	
" 222	" "	10	-	-	-	-	-	-	
" 111	" "	**5**	-	-	-	-	-	-	
Pen 321	Dic/Ris	5	-	-	-	-	-	-	D3
" 421	Dic odo	4	-	-	-	-	-	-	
Nuw 111	Dic zub	**30**	-	-	-	-	-	-	
" 211	Dic 2spp	3	-	-	-	-	-	-	
Qua 111	" "	**20**	-	-	-	-	-	-	
Mak 111	" "	1	-	-	-	-	-	-	
Moo 111	Dic zub	5	-	-	-	-	-	-	
Mng 111	Dic 2spp	6	-	-	-	-	-	-	
Qac 111	Hei/Dic	8	-	-	-	-	-	-	
Bir 211	Sph 2spp	**95**	-	-	-	-	-	-	
" 311	Hei/Sph	**40**	-	-	-	-	-	-	
" 111	Sph 2spp	**85**	-	-	-	-	-	-	
Mol 111	Sph pon	**99**	-	-	-	-	-	-	
Tin 121	Sph 2spp	**95**	-	-	-	-	-	-	S
Wal 111	Dic odo	**3**	-	-	-	-	-	-	
Kle 211	Sph pon	**100**	-	-	-	-	-	-	
Kul 111	" "	**99**	-	-	-	-	-	-	
Aas 411	Dic/Sph	**30**	14	-	13	-	-	1	
" 511	Dic elo	**20**	-	-	-	-	-	-	
Gre 111	Sph pon	**85**	-	-	-	-	-	-	E
Lut 311	" "	29	1	-	-	-	1	-	
Kle 111	Hei/Dic	8	-	-	-	-	-	-	H
Aas 111	Hei elo	1	-	-	-	-	-	-	
" 311	" "	9	-	-	-	-	-	-	
Ask 111	Equ sp	1	-	-	-	-	-	-	E
Lut 211	" "	**10**	-	-	-	-	-	-	
Total TCs		43	4	2	1	1	1	1	
Total indivs		%	24	8	13	1	1	1	

Tab. 47. *Hamshawvia/Sphenobaiera*, Molteno occurrence; emphasizing habitat

Habitat:
D1—*Dicroidium* riparian forest (type 1)
D2—*Dicroidium* riparian forest (type 2)
D3—*Dicroidium* open woodland
S—*Sphenobaiera* closed woodland
H—*Heidiphyllum* thicket
E—Equisetum marsh
?—uncertain

Gondwana Triassic occurrence (elaborated)

Together with *Dicroidium* and *Heidiphyllum*, *Sphenobaiera* is one of the three clearly dominant gymnosperm foliage genera in the Molteno and Gondwana Triassic. Its supposed female-fruit affiliate, *Hamshawvia*, remains, however, a rarity and is known outside the Molteno from only a single specimen in South America and two from Australia.

South America

Frenguelli (1942) described *Umkomasia cacheutensis*, based on a single good specimen from the 'Estratos con *Estheria*' in the Cacheuta Fm., Upper Triassic of Argentina. HMA has been able to study this specimen in La Plata (1999) and verify that it is definitely not an *Umkomasia*. It is placed here in our new genus as *Hamshawvia cacheutensis* (Frenguelli 1942) And. & And., comb. nov. This is the only individual known from South America. Specimens from the Molteno show a similar radiating pattern around the ovules—see PRE/F/21438a, p. 215, tf. 5; pl. 70(7).

Australia

Holmes [1995, pl. 1(1)] illustrated two individuals of a 'paired ovulate organ' from the Nymboida Coal Mine Quarry (see Holmes 2000) of the Middle Triassic (Ladinian) Basin Creek Fm., Nymboida Coal Measures, New South Wales. The two clear impressions/compressions (no cuticle) occur on a single slab along with a number of *Sphenobaiera* leaves and a couple of specimens each of *Dicroidium* and *Heidiphyllum*. The rarity of this fruit is confirmed by the fact that these are the only specimens observed by Holmes (pers. comm.) despite his comprehensive collecting from the Nymboida locality over many years.

Comparisons beyond Gondwana Triassic

Laurasian Triassic

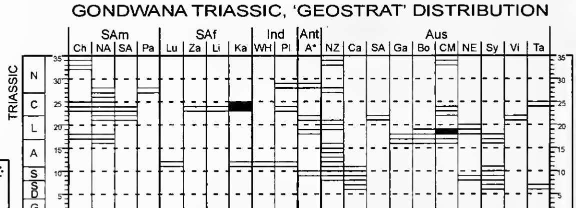
Hamshawvia has similarities with *Leuthardtia* and *Haitingeria* (both Upper Triassic, Europe) and regarded by Crane (1986) as probable microsporophylls. However, Meyen (1988) links *Leuthardtia* to *Stiphorus* and considers it female.

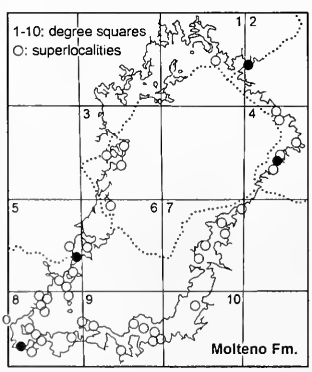
Irania hermaphroditica from the Rhaetic of Iran, described by Schweitzer (1977), has paired megasporophylls and microsporangial strobili attached to an axis. The once-forked axis with paired megasporophylls is similar to *Hamshawvia* but differs in the discs being uniovulate with basal placentation and nonfleshy. The microsporangia have been compared to those of the extant *Ginkgo biloba* and the affiliated leaves are possibly *Desmiophyllum armani*.

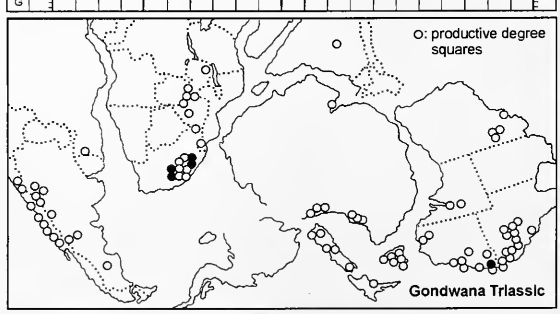
Other ages

Stiphorus is close to *Hamshawvia*—clearly affiliated with *Glossophyllum*—as described by Meyen (in Gomankov & Meyen 1986) from the *Tatarina*-flora (Late Permian of Eurasia). *Stiphorus* is also a strobilus with a once-forked pair of megasporophylls. It differs in the ovules (seeds) being attached externally and not embedded in the fleshy lamina.

GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION







Evidence for affiliation of organs

The measure of our uncertainty as to which ovulate fruit affiliates with the diverse and abundant foliage genus *Sphenobaiera* was first outlined in some detail in And. & And. (1989, p. 132).

Kindred reinforcement

Meyen (1982 1986, 1987, 1988) reported the forked ovulate genus *Stiphorus* (closely comparable to *Hamshawvia*) as securely affiliating with *Glossophyllum* in the *Tatarina*-flora; and with 'leafy shoots, *Kirjamkenia lobata*, producing both entire (*Glossophyllum*-like) and palmately dissected (*Sphenobaiera*-like) leaves', from the Permo-Triassic of Siberia. Meyen (1988) also found *Leuthardtia*, 'similar, if not identical' to *Stiphorus*, thus securely linking *Sphenobaiera*-like leaves in the Triassic of Switzerland (the Basel flora of Kräusel & Schaarschmidt 1966) with *Glossophyllum* leaves from the Donets basin.

Mutual occurrence

Hamshawvia is infrequent, occurring in only four Molteno TCs, but each of these does yield *Sphenobaiera*, even if not in high abundance, i.e. Aas 411 with 30%, Umk 111 5%, Lit 111 1% and Lut 111 less than 1%. *Ginkgoites* is a less likely contender as it does not occur at Umk 111 and Lut 111, while at Aas 411 and Lit 111 it is below 1%. The possibility of *Avatia* instead of *Hamshawvia* affiliating with *Sphenobaiera* is also less likely, as it does not occur at Umk 111 and Lit 111. However, *Avatia* is very common (over 50 individuals) at Aas 411 and Bir 111, which both yield high *Sphenobaiera* percentages and low *Ginkgoites* percentages. *Fanerotheca*, as we originally considered, could also be a contender for affiliation with *Sphenobaiera* on the sole basis of recorded Molteno co-occurrences (Tab. 48).

Holmes (1995) illustrated two clearly preserved, paired ovulate organs, almost certainly identifiable as *Hamshawvia*, from the Middle Triassic Nymboida Coal Measures, Australia. These appeared on a bedding-plane along with a number of *Sphenobaiera* leaves.

Organic attachment

A single specimen (Aas 411, PRE/F/12823a,b; pl. 71) from the Molteno shows four *Sphenobaiera* leaves and a bifurcating fructification clearly attached terminally to a short shoot. The forked axis of the organ is distinct but the two megasporophyll heads are small and not well preserved. We consider them to be immature fruits. The heads as preserved are one half the size of those of *Avatia* and one third the size of *Hamshawvia*. We accept that this attached fruit could possibly be *Avatia* but more likely it is *Hamshawvia*. Because of the uncertainty of identification, we have recorded this affiliation as Grade 4/5.

Cuticular correspondence

The cuticle of *Hamshawvia* [tfs 3, 4, p. 211; pls 67(3–9), 68(4–7), 69(4, 5)] from both Lit 111 and Umk 111, is similar to that of *Sphenobaiera*, notably in the thickness and quality of preservation, the strongly papillate cells with gently curved walls, and in the clear ring of lappetate subsidiary cells. No cuticle is known from *Avatia*.

Adaptive radiation (Molteno diversity)

Hamshawvia, though both infrequent and rarely preserved, was evidently diverse. Four of the five small Molteno palaeodemes at hand represent distinct species. These are differentiated by peduncle length and particularly the number and arrangement of ovules. Two of the species derive from a single TC (Umk 111), while the others are from very different habitats and stratigraphic levels.

H. baccata—Umk 111 Dic 2 spp (Umkomaas Valley), 6 indivs
Dicroidium riparian forest (mature); Cycle 2b (Indwe Member)
H. longipedunculata—Aas 411 Dic/Sph, (Aasvoëlberg), 14 indivs
Sphenobaiera closed woodland; Cycle 1 (Bamboesberg Member)
H. octosemina—Umk 111 Dic 2 spp (Umkomaas Valley), 1 indiv.
Dicroidium riparian forest (mature); Cycle 2b (Indwe Member)
H. linisemina—Lut 311 Hei elo (Lutherskop); 1 indiv.
Heidiphyllum thicket; Cycle 3 (Mayaputi Member)

	Genera							Species				
assemblages (taphocoenosis)	*Sphenobaiera*	♀ *Hamshawvia*	♂ *Stachyopitys*	♀ *Fanerotheca*	♀ *Fanerotheca* seeds	♀ *Avatia*	♀ *Avatia* seeds	*H. baccata*	*H. longipedunculata*	*H. octosemina*	*H. linisemina*	*H.* spp. indet
Nav 111 Dic odo	-	-	-	1	-	-	-	-	-	-	-	-
Cal 111 Dic/Sph	**44**	-	-	-	-	-	-	-	-	-	-	-
Bir 211 Sph 2spp	**95**	-	-	1	-	-	-	-	-	-	-	-
311 Hei/Sph	**40**	-	1	2	✓	1	-	-	-	-	-	-
111 Sph 2spp	**85**	-	113	60	✓✓✓	66	✓✓✓	-	-	-	-	-
Gre 111 Sph pon	**85**	-	1	4	✓	-	-	-	-	-	-	-
Boe 111 Lep sto	-	-	-	1	-	-	-	-	-	-	-	-
Cyp 111 Dic cra	-	-	44	1	-	-	-	-	-	-	-	-
Mol 111 Sph pon	**99**	-	-	1	-	-	-	-	-	-	-	-
Kan 112 Hei elo	-	-	5	-	-	-	-	-	-	-	-	-
Tel 111 "	-	-	45	2	✓	-	-	-	-	-	-	-
Kom 111 Sph/Dic	**60**	-	-	2	✓	-	-	-	-	-	-	-
Vin 111 Dic odo	4	-	5	-	-	-	-	-	-	-	-	-
Ela 111 "	**1**	-	8	1	✓	-	-	-	-	-	-	-
Kra 311 "	-	-	8	-	-	-	-	-	-	-	-	-
Kra 111 "	1	-	2	-	-	-	-	-	-	-	-	-
Lut 311 Hei elo	29	1	19	7	✓✓✓	3	3?	-	-	-	1	-
211 Equ sp.	**10**	-	-	-	-	-	-	-	-	-	-	-
Tin 121 Sph 2spp	**95**	-	1	1	✓✓	1	-	-	-	-	-	-
Wal 111 Dic odo	**3**	-	21	24	✓✓✓	-	-	-	-	-	-	-
Kon 223 "	1	-	-	-	-	-	-	-	-	-	-	-
222 "	10	-	35	1	-	-	-	-	-	-	-	-
111 "	**5**	-	-	-	-	-	-	-	-	-	-	-
Pen 321 Dic/Ris	5	-	2	-	-	-	-	-	-	-	-	-
421 Dic odo	4	-	-	-	-	-	-	-	-	-	-	-
Kle 111 Hei/dic	8	-	3	1	✓✓	-	-	-	-	-	-	-
211 Sph pon	**100**	-	-	-	-	-	-	-	-	-	-	-
Kul 111	**99**	-	-	-	-	-	-	-	-	-	-	-
Kap 111 Dic/Ris	20	-	35	40	✓✓✓	-	-	-	-	-	-	-
Nuw 111 Dic zub	**30**	-	-	-	-	5	✓✓	-	-	-	-	-
211 Dic 2spp	3	-	-	-	-	-	-	-	-	-	-	-
Mor 111 Dic odo	-	-	30	-	-	-	-	-	-	-	-	-
Qua 111 "	**20**	-	-	-	-	-	-	-	-	-	-	-
Mak 111 "	1	-	-	-	-	-	-	-	-	-	-	-
Maz 111 Dic cra	**12**	-	5	6	✓✓✓	-	-	-	-	-	-	-
211 Hei/Dic	**1**	-	26	5	✓✓✓	-	-	-	-	-	-	-
Moo 11 Dic zub	5	-	-	-	-	-	-	-	-	-	-	-
Hla 211 Dic 3spp	7	-	-	3	-	-	-	-	-	-	-	-
212 "	7	-	-	-	-	-	-	-	-	-	-	-
213 Dic elo	49	-	2	3	✓	-	-	-	-	-	-	-
Umk 111 Dic 2spp	**5**	7	19	30	✓✓✓	-	-	6	-	1	-	-
San 111 Dic cra	-	-	5	5	✓	-	-	-	-	-	-	-
Mng 111 Dic 2spp	6	-	-	-	-	-	-	-	-	-	-	-
Qac 111 Hei/Dic	8	-	2	-	-	-	-	-	-	-	-	-
Mat 111 Dic dub	18	-	31	6	✓	-	-	-	-	-	-	-
Lit 111 Dic/Hei	**1**	2	4	3	-	-	-	2	-	-	-	-
Aas 111 Hei elo	1	-	-	-	-	-	-	-	-	-	-	-
311 "	9	-	-	-	-	-	-	-	-	-	-	-
411 Dic/Sph	**30**	14	67	47	✓✓✓	38	7	-	13	-	-	1
511 Dic elo	**20**	-	-	-	-	-	-	-	-	-	-	-
Ask 111 Equ sp	**1**	-	-	-	-	-	-	-	-	-	-	-
Total TCs	43	4	27	26	17	6	4	2	1	1	1	1
Total indivs	%	24	539	247	✓	114	✓	8	13	1	1	1

Tab. 48. *Hamshawvia*/*Sphenobaiera*, Molteno occurrence; emphasizing species diversity

Hamshawvia baccata J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: BP/2/1124a,b; pls 66(1–4), 67(10, 11).
Assemblage (TC): Umk 111 Dic 2spp, Umkomaas Valley.
Preservation: complete strobilus, part and counterpart; compression, in thinly laminated, carbonaceous (good cuticle), moderately baked, dark grey shale with good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 6 indivs (3 intact, 3 partial), pls 66, 67.

Sister palaeodemes—1 (as listed)
Lit 111 Dic/Hei: 2 indivs (2 intact), pl. 68.

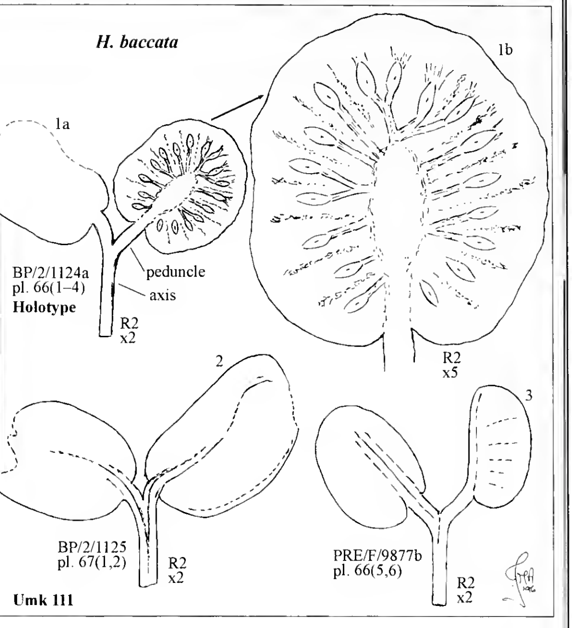
Specific diagnosis
A *Hamshawvia* species with a short axis and megasporophylls with *ca* 17 ovules radially arranged about a fusiform median vein.

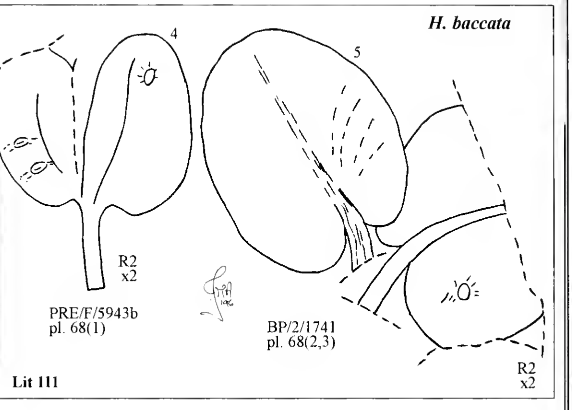
Specific characters
Strobilus: axis short, *ca* 6 mm to bifurcation.
Megasporophyll: lamina spherical to broadly ovate, with *ca* 17 ovules arranged radially about a fusiform vein and connected to simple or forked vascular traces.
Ovule/seed: elliptical.

Etymology
baccata—bacca (Lat.), berry, berry-like, with reference to the appearance of the megasporophyll heads.

Comments & comparison
H. baccata is based on two palaeodemes, but particularly that from Umk 111, representing *Dicroidium* riparian forest. The diagnostic arrangement and number of ovules seen in the holotype are obscure in the additional five specimens from Umk 111, which are preserved in varied orientation. However, the additional specimens are similar in size, form and texture. PRE/F/9877b (tf. 3) shows one megasporophyll in a closed position folded along the median rib.

Though not much detail can be discerned in the two Lit 111 specimens, tfs 4, 5 adjacent and pl. 68(1, 2), they are tentatively placed in this species. They also appear to show ovules with a radiating pattern as in the Umk 111 holotype, and are generally similar in shape and size, and in the form of the peduncle and pedicel.





Hamshawvia octosemina J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/769; pl. 69(1–7).
Assemblage (TC): Umk 111 Dic 2spp, Umkomaas Valley.
Preservation: incomplete megasporophyll, without counterpart; compression, in thinly laminated, carbonaceous (good cuticle), moderately baked, dark grey shale with good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimen: 1 indiv (partial); pl. 69(1–7).

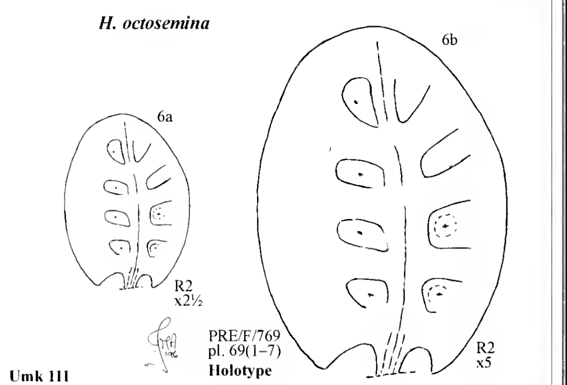
Sister palaeodemes—nil.

Specific diagnosis
A *Hamshawvia* species with megasporophylls bearing 8 ovules (in rounded-rectangular fields) arranged in rows of 4 on either side of a median vein.

Specific characters
Strobilus: axis unknown.
Megasporophyll: lamina ovate, with 8 ovules in rounded-rectangular seminal fields, arranged in rows of 4 on either side of a median vein.
Ovule/seed: shape unknown.

Etymology
octosemina—referring to the eight ovules in each megasporophyll.

Comments & comparison
Though based on a single specimen, the diagnostic characters of *H. octosemina* are clear. The species very evidently comes closest to *H. linisemina*.



Hamshawvia longipedunculata J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/21778a,b; pl. 70(1–3).
Assemblage (TC): Aas 411 Dic/Sph, Aasvoëlberg.
Preservation: nearly complete strobilus, part and counterpart; 3D impression, in thinly laminated, strongly baked, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 13 indivs (2 intact, 11 partial), pl. 70(1–10).

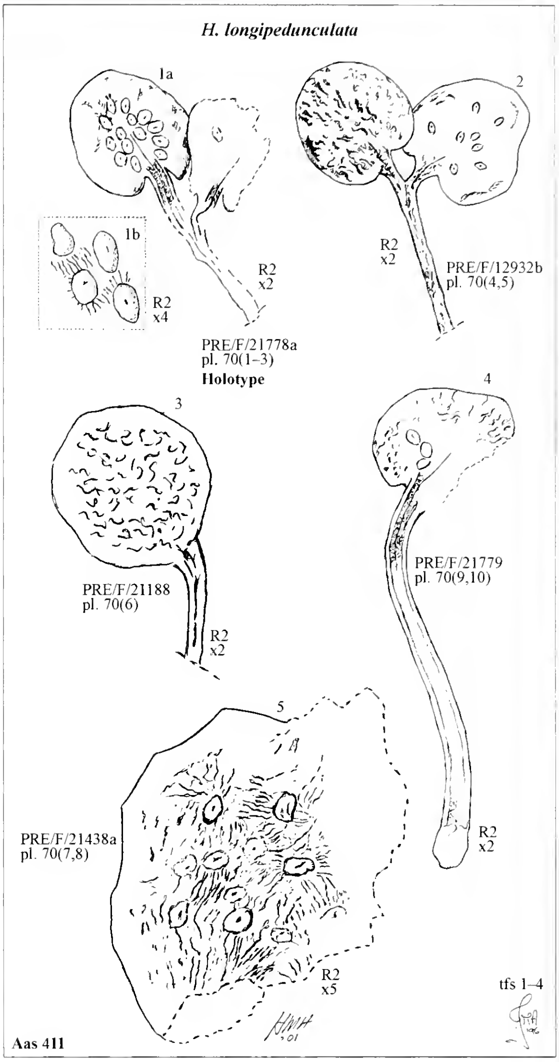
Sister palaeodemes—nil.

Specific diagnosis
A *Hamshawvia* species with a long axis and megasporophylls with *ca* 14 ovules in an irregular radial arrangement about a median vein.

Specific characters
Strobilus: axis elongated, *ca* 25–30 mm to bifurcation.
Megasporophyll: lamina circular, surface wrinkled, with *ca* 14 ovules in irregular radial arrangement about an obscure median vein.
Ovule/seed: oval.

Etymology
longipedunculata—referring to the elongated peduncle (actually axis) of the strobilus.

Comments & comparison
H. longipedunculata differs from *H. baccata* in the elongate peduncle and more random arrangement of the ovules in the megasporophyll lamina. Specimen PRE/F/21438a, tf. 5, shows best the characteristic radiating pattern around the ovules found in this species. The feature probably relates to differential shrinkage between the ovules and surrounding tissue through dehydration before or during fossilisation.



Hamshawvia linisemina J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/11607; pl. 69(8–10).
Assemblage (TC): Lut 311 Hei elo, Lutherskop.
Preservation: incomplete strobilus, without counterpart; impression, in thickly laminated, medium grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimen: 1 indiv. (intact), pl. 69(8–10).

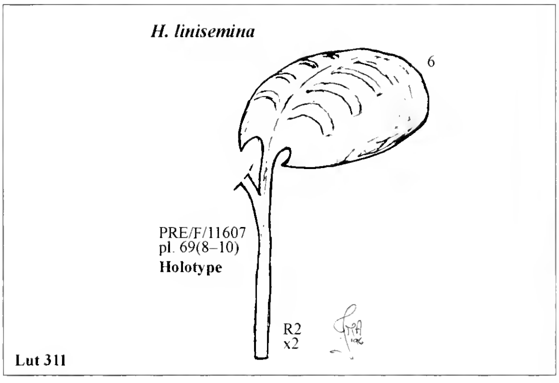
Sister palaeodemes—nil.

Specific diagnosis
A *Hamshawvia* species with an intermediate-length axis and megasporophylls with *ca* 10 ovules (in linear-rectangular fields), arranged in rows of 5 on either side of a median vein.

Specific characters
Strobilis: axis intermediate, *ca* 13 mm to bifurcation.
Megasporophyll: lamina ovate, with *ca* 10 ovules in linear-rectangular seminal fields arranged in rows of 5 on either side of a median vein.
Ovule/seed: shape unknown.

Etymology
linisemina—referring to the linear-rectangular seminal fields.

Comments & comparison
The Lutherskop (Lut 311) palaeodeme on which this species is based consists of a single imperfect specimen. Even so, following our taxonomic guidelines, we feel its identification justified. The specimen falls readily in the genus *Hamshawvia* and is most like the single specimen of *H. octosemina* from Umk 111. The distinguishing feature of *H. linisemina* is the linear-rectangular—in contrast to roundly rectangular—areas demarcating the seeds. This feature is not as clear as in the Umk 111 specimen and could be misinterpreted. In support of recognising a separate species is the differing habitat: Umk 111 has been interpreted as representing *Dicroidium* riparian forest, and Lut 311 *Heidiphyllum* thicket. Should this be correct, it is more likely that we are dealing with two species than one.



Stachyopitys A.Schenck 1867

Type species
Stachyopitys preslii A.Schenck 1867.
Strullendorf, near Bamberg, Bavaria; Rhaetic, Triassic.

Generic concept
A ginkgoopsid male strobilus of lax spicate to bushy form, with simple to branched microsporophylls bearing terminal spherical heads of radiating microsporangia.

Generic characters (Molteno Fm.)
Attachment: strobilus borne singly on a bulbous short shoot which dehisces as a unit.
Strobilus: simple, lax, spicate to bushy, radially symmetrical, small to large (25–>150 mm); axis gracile, gently curving to sinuous; microsporophylls numerous, irregularly helical.
Microsporophyll: simple to irregularly branched and bushy, radially symmetrical; peduncle gracile; fertile heads one to several, pedicelate; microsporangia in lax to dense fascicles, few to numerous per head.
Microsporangium: irregularly elliptical to spathulate (0.5–3 mm long); ornamentation fine, linear, sinuous, forking and converging.

Etymology
Stachyopitys—stachys (Gr.), spike; *pitys* (Gr.), a pine.

Global range: numerous spp., Pangaea, Tr.–K.

Gondwana Triassic occurrence
SAm—Argentina, 2 TCs (8 indivs).
SAf—Karoo Basin, 27 TCs (539 indivs).
Aus—Queensland, Victoria, N.Z., 7 TCs (10 indivs).

Molteno occurrence
Frequency (F): 27 TCs (of 100 sampled in Molteno).
Diversity (D): 6 species.
Abundance (A): 539 individuals, rare to very rare in top 8 TCs.

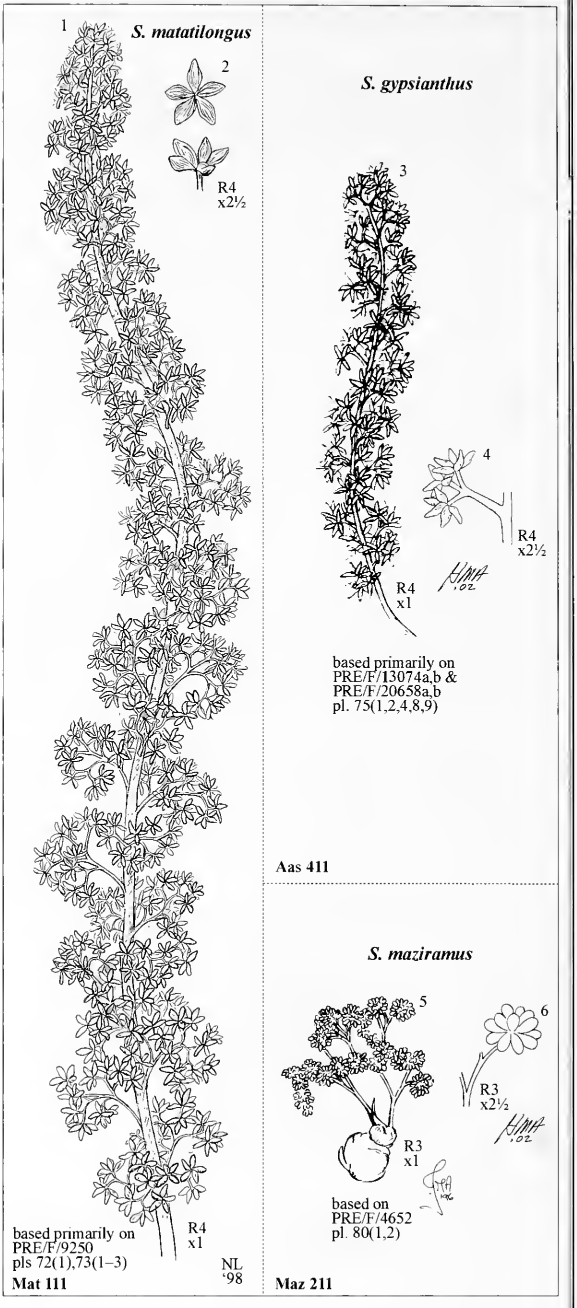
Kon 222 Dic odo:	35 indivs in	40 man-hrs cleaving	(9 per 1 man-day)	rare
Mat 111 Dic dub:	31 " "	65 " "	(5 " 1 ")	"
Cyp 111 Dic cra:	44 " "	100 " "	(>5 " 1 ")	"
Tel 111 Hei elo:	45 " "	90 " "	(4 " 1 ")	"
Wal 111 Dic odo:	21 " "	50 " "	(4 " 1 ")	"
Maz 211 Hei/Dic:	26 " "	85 " "	(4 " 1 ")	"
Bir 111 Sph 2spp:	113 " "	550 " "	(>2 " 1 ")	"
Aas 411 Dic/Sph:	67 " "	512 " "	(>1 " 1 ")	v. rare

Though never common, *Stachyopitys* is the most frequently occurring gymnospermous microsporangiate genus in the Molteno. Its affiliate, *Sphenobaiera*, is the third most prominent foliage genus in the Gondwana Triassic.

Affiliated organs
Female strobilus: *Hamshawvia*—Grade 4 (Mut. occ., Kin. reinf.).
Foliage: *Sphenobaiera*—Grade 5 (Org. att.).

Classification & comparison
Suprageneric classification (Hamshawviaceae/Hamshawviales)
From the evidence of the single Molteno specimen (p. 220, tf. 10a,b) showing the attachment of *Stachyopitys* (male) and *Sphenobaiera* (foliage) to a common base, together with the well established affiliations of both to *Hamshawvia* (female), we have an unusually soundly based whole-plant genus. Following the arguments outlined for *Hamshawvia* (p. 210), this combined taxon is placed in the family Hamshawviaceae and order Hamshawviales within the class Ginkgoopsida.

Intergeneric comparison (Gondwana Triassic)
Stachyopitys is closest to the microsporangiate genera *Antevsia* and *Pteruchus* (particularly *P. africanus*). While complete, well-preserved specimens of these three genera can be readily distinguished, fragmentary or poorly preserved individuals may be confused. *Antevsia* (from the Molteno) differs in bearing its relatively few microsporangia in sessile lateral fascicles on projecting flanges along the microsporophylls, and *Pteruchus* in its more numerous microsporangia borne abaxially on laminate heads.



Reconstructions
The *Stachyopitys* strobilus, based on many well-preserved Molteno palaeodemes, is clearly spicate rather than planate in form. The remarkable bulbous base, found in many specimens through several palaeodemes (notably Bir 111, Wal 111, Maz 111, Maz 211), appears to represent a kind of specialised short shoot. We have made a reconstruction of the single specimen (PRE/F/4000, p. 211, tf. 2) in which a *Stachyopitys* (*S. lacrisporangia*) strobilus and a *Sphenobaiera* (*S. sectina*) leaf are found mutually attached to a bulbous base [pl. 81(1–6)]. Reconstructions are also provided for three of the six Molteno *Stachyopitys* species.

Gondwana Triassic occurrence (elaborated)

Numerous supposed *Stachyopitys* specimens have been recorded from Gondwana (Tab. 49), but some are here placed in *Pteruchus* (Tab. 64). Only *S. simmondsii* from Queensland, based on a complete strobilus, is accepted by us as a valid species. The remainder, based only on fragmentary strobili, are regarded as indeterminate at species level. *S. simmondsii* is closest to *S. maziramus* in size and the attachment to a bulbous base, but differs in the simple (unbranched) axis and a greater number of sporangia per head.

Adaptive radiation (Molteno diversity)

Though we have differentiated six species of *Stachyopitys*, they are less readily defined than in the putative female (*Hamshawvia*, four species) and foliage (*Sphenobaiera*, nine species) affiliates. The genus is both frequent, occurring in 27 TCs, and relatively common, with some 500 curated specimens, but morphologically it is notably conservative. The diagnostic characters lie chiefly in the shape and size of the strobilus, together with the shape, size and number of microsporangia per microsporophyll head. The species showing the greatest frequency is *S. lacrisporangia*, which occurs in 23 TCs.

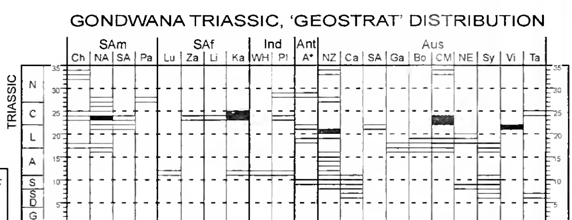
The species derive equally from *Dicroidium*- and *Sphenobaiera*-dominated habitats and from various stratigraphic levels:

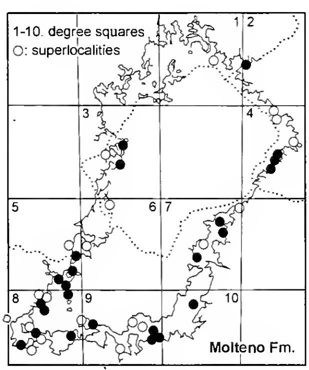
S. matatilongus—Mat 111 Dic dub (Matatiele), 15 indivs
Dicroidium riparian forest (immature); Cycle 2b (Indwe Member)
S. matatiramus—Mat 111 Dic dub (Matatiele), 16 indivs
Dicroidium riparian forest (immature); Cycle 2b (Indwe Member)
S. gypsianthus—Aas 411 Dic/Sph (Aasvoëlberg), 44 indivs
Sphenobaiera closed woodland; Cycle 1 (Bamboesberg Member)
S. lacrisporangia—Bir 111 Sph 2spp (Birds River), 57 indivs
Sphenobaiera closed woodland; Cycle 5 (Tsomo Member)
S. rotundisporangia—Bir 111 Sph 2spp, (Birds River), 3 indivs
Sphenobaiera closed woodland; Cycle 5 (Tsomo Member)
S. maziramus—Maz 211 Hei/Dic (Mazenod), 1 indiv.
Dicroidium riparian forest (immature); Cycle 2c (Indwe Member)

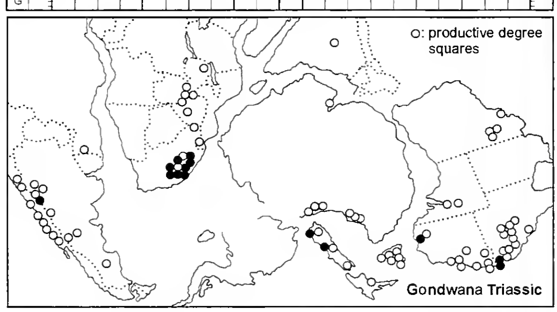
Tab. 49.

***STACHYOPITYS* HYPODIGM, Gondwana Triassic occurrence**

AUTHOR		SUBREGION		FORMATION		LOCALITY	NAME	Indivs	ILLUSTRATION	Species: Molteno: *S. matatilongus*	*S. matatiramus*	*S. gypsianthus*	*S. lacrisporangia*	*S. rotundisporangia*	*S. maziramus*	*S. spp.*	Intact-ness: Intact strobili	Fragmentary "	Isolated megasp.
SOUTH AMERICA																			
1944c	Frenguelli	Cacheuta	NA4	24	Potrerillos	YPF old admin. bld.	*Stachyopitys anthoides*	6	pl 1(1-5), 2(1-2), f 1	-	-	-	-	-	-	6	-	3	3
1967	Jain & Del.	"	"	"	"	Minas de Petrolea	" "	2	pl 90(16), pl 96(12-13)	-	-	-	-	-	-	2	-	1	1
SOUTH AFRICA																			
1903	Seward	Matatiele	KA7	24	Molteno	Kenigha River	*Stachyopitys sp.*	1	pl 9(2)	-	-	-	-	-	-	1	-	1	-
1978-1999 Anderson & Anderson Molteno literature not included in this table																			
NEW ZEALAND																			
1981b	Retallack	Benmore Dam	NZ4	21	Long Gully	Long Gully	*Townrovia petasata*	1	pl 11(E), f 3(C)	-	-	-	-	-	-	1	-	1	-
1985	"	Southland	NZ6	?		Mataura Is F47/f7572	*Antevsia sp.*	1	f 7(7)	-	-	-	-	-	-	1	-	1	-
AUSTRALIA																			
1898	Shirley	Ipswich/Esk.	CM5	24	Blackstone Stage	Denmark Hill (loc 39)	*Stachyopitys simmondsi*	1	pl 18(2)	-	-	-	-	-	-	1	1	-	-
1927	Chapman	Victoria	Vi2	22	?	Bald Hill	" cf. *annularioides*	1	pl 11(25)	-	-	-	-	-	-	1	-	-	1
1917	Walkom	Ipswich/Esk.	CM5	24	Blackstone Stage	Nundah	" *annularioides*	1	pl 4(6)	-	-	-	-	-	-	1	-	1	-
1962	Townrow (specimen repeated from Shirley 1898)						" *simmondsi*	*	pl 24(2)	-	-	-	-	-	-	*	*	-	-
1965	"	Hamilton	Ta?	?	?	Langloh Coal Mine	*Pteruchus petasatus*	6	pl 1(B), 14(A-F)	-	-	-	-	-	-	6	1	2	3
"	Hill *et al.*	Brisbane	CM6	23	Tingalpa	Petrie's Quarry	" *simmondsi*	1	pl T6(5)	-	-	-	-	-	-	1	1	-	-







assemblages (taphocoenosis)		Genera							Species								Intactness		
		Sphenobaiera	♀ *Hamshawvia*	♀ *Fanerotheca*	♀ *Faner.* seeds	♀ *Avatia*	♀ *Avatia* seeds	♂ *Stachyopitys*	*S. matatilongus*	*S. matatiramus*	*S. gypsianthus*	*S. lacri.* (robust)	*S.* (slender)	*S. rotundisporangia*	*S. maziramus*	*S.* spp indet	Intact strobili	Partial strobili	Isolated microsp.
Nav 111	Dic odo	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cal 111	Dic/Sph	**44**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bir 211	Sph 2spp	**95**	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
311	Hei/Sph	**40**	-	2	✓	1	-	1	-	-	-	-	1	-	-	-	-	1	-
111	"	**85**	-	60	✓✓✓	66	✓✓✓	113	-	-	-	53	57	3	-	-	84	22	7
Gre 111	Equ sp	**85**	-	3	✓	-	-	1	-	-	-	-	-	-	-	1	-	1	-
Boe 111	Lep sto	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cyp 111	Dic cra	-	-	1	-	-	-	44	-	-	-	-	44	-	-	-	6	13	25
Mol 111	Sph pon	**99**	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kan 112	Hei elo	-	-	-	-	-	-	5	-	-	-	-	5	-	-	-	-	3	2
Tel 111	"	-	-	2	✓	-	-	45	-	1	-	44	-	-	-	-	21	17	7
Kom 111	Sph/Dic	**60**	-	2	✓	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vin 111	Dic odo	4	-	-	-	-	-	5	-	-	-	5	-	-	-	-	-	3	2
Ela 111	"	**1**	-	1	✓	-	-	8	-	-	-	-	8	-	-	-	-	7	1
Kra 311	"	-	-	-	-	-	-	8	-	-	-	8	-	-	-	-	-	5	3
111	"	1	-	-	-	-	-	2	-	-	-	2	-	-	-	-	-	1	1
Lut 311	Hei/Dic	29	1	7	✓✓✓	3	3?	19	-	-	10	9	-	-	-	-	4	11	4
211	Equ sp.	**10**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tin 121	Sph 2spp	**95**	-	1	✓✓	1	-	1	-	-	-	-	1	-	-	-	-	1	-
Wal 111	Dic odo	**3**	-	24	✓✓✓	-	-	21	-	-	-	20	-	-	-	1	8	8	5
Kon 223	"	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
222	"	10	-	1	-	-	-	35	-	-	1	-	34	-	-	-	4	21	10
111	"	**5**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pen 321	Dic/Ris	5	-	-	-	-	-	2	-	-	-	-	-	-	-	2	-	2	-
421	Dic odo	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kle 111	Hei/Dic	8	-	1	✓✓	-	-	3	-	-	-	-	3	-	-	-	1	2	-
211	Sph pon	**100**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kul 111	"	**99**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kap 111	Dic/Ris	20	-	40	✓✓✓	-	-	35	-	-	-	-	35	-	-	-	10	17	8
Nuw 111	Dic zub	**30**	-	-	-	5	✓✓	-	-	-	-	-	-	-	-	-	-	-	-
211	Dic 2spp	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mor 111	Dic zub	-	-	-	-	-	-	30	-	-	-	30	-	-	-	-	12	14	4
Qua 111	Dic odo	**20**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mak 111	"	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Maz 111	Dic cra	**12**	-	6	✓✓✓	-	-	5	-	-	-	1	-	-	-	4	1	-	4
211	Hei/Dic	**1**	-	5	✓✓✓	-	-	26	-	-	-	25	-	-	1	-	5	7	14
Moo 111	Dic zub	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hla 211	Dic 3spp	7	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
212	"	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
213	Dic elo	49	-	5	✓	-	-	2	-	-	-	-	2	-	-	-	-	2	-
Umk 111	Dic 2spp	**5**	7	16	✓✓✓	-	-	19	-	-	-	16	-	-	-	3	5	12	2
San 111	Dic cra	-	-	5	✓	-	-	5	1	-	-	4	-	-	-	-	3	2	-
Mng 111	Dic 2spp	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Qac 111	Hei/Dic	8	-	-	-	-	-	2	-	-	-	-	-	-	-	2	-	2	-
Mat 111	Dic dub	18	-	6	✓	-	-	31	15	16	-	-	-	-	-	-	17	13	1
Lit 111	Dic/Hei	**1**	2	3	-	-	-	4	-	-	-	-	-	-	-	4	-	2	2
Aas 111	Hei elo	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
311	"	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
411	Dic/Sph	**30**	14	47	✓✓✓	38	7	67	-	-	44	16	-	7	-	-	32	27	8
511	Dic elo	**20**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ask 111	Equ sp.	**1**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total TCs		43	4	26	17	6	4	27	2	2	3	13	10	2	1	7	15	26	19
Total indivs		%	24	247	✓	114	✓	539	16	17	55	233	190	10	1	17	213	216	110

Tab. 50. *Stachyopitys*, Molteno occurrence

Evidence for affiliation of organs

Organic attachment

The unique specimen (PRE/F/4000, pl. 81) from Maz 111 Dic cra shows the lower portion of a *Sphenobaiera* leaf and part of a *Stachyopitys* strobilus clearly attached to a common bulbous base and is thus given a Grade 5 affiliation. The leaf is close to *Sphenobaiera africana* (for further leaves from Maz 111, see And. & And. 1989; pls 97, 98) and the strobilus to *Stachyopitys lacrisporangia.*

The only other known specimen involving related taxa in apparent organic connection was described by Yang (1986) from China (Xujanhe Fm. in Xing-Long, Wan-Gu region of Dazu, Sichuan). The male strobilus was close to *Stachyopitys* and has been named *Sphenobaieroanthus sinensis*. The exact nature of attachment is difficult to discern from the photographs, but certainly there is a clear shoot with numerous *Sphenobaierocladus sinensis* leaves attached.

Mutual occurrence

The most convincing instance of co-occurrence is at Bir 111 where *Sphenobaiera* comprises 85% of the assemblage and *Stachyopitys* is represented by 113 catalogued specimens (Tab. 50). Similar good associations are recorded from Aas 411 and Umk 111. Some of the *Stachyopitys* species are possibly affiliated with *Fanerotheca* which also occurs in high numbers at Bir 111, Aas 411 and Umk 111 (see also Wal 111, Kap 111, Lut 111). For further discussion consult affiliation text under *Fanerotheca*. Another uncertainty is that there are six TCs where *Stachyopitys* is present but *Sphenobaiera* is absent, i.e. Cyp 111, Tel 111, San 111, Kra 311, Mor 111, Kan 112. *Fanerotheca* appears at the first three of these TCs.

Kindred reinforcement

Associations of *Sphenobaiera* and *Stachyopitys* were recorded from the Basel flora, Switzerland (Keuper, Upper Triassic), by Leuthardt (1903). From the Early Liassic of Bayreuth, Germany, Kirchner & Van Konijnenburg-Van Cittert (1994) described the female organ *Schmeissneria microstachys* attached as a fascicle with numerous simple elongate leaves to a short shoot. This unique genus is considered by them to be of ginkgoalean affinity. They regarded the affiliated male as *Stachyopitys preslii* (not yet found attached). It was conceded that 'there may be other plants within the Ginkgoales carrying *Stachyopitys* fructifications'.

Stachyopitys matatilongus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/9250a,b; pls 72(1), 73(1–3).
Assemblage (TC): Mat 111 Dic dub, Matatiele.
Preservation: intact strobilus, tip and base missing, part and counterpart; impression, in thickly laminated, olive-grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 15 indivs (6 intact, 8 partial, 1 isolated), pls 72(1–4), 73(1–6).

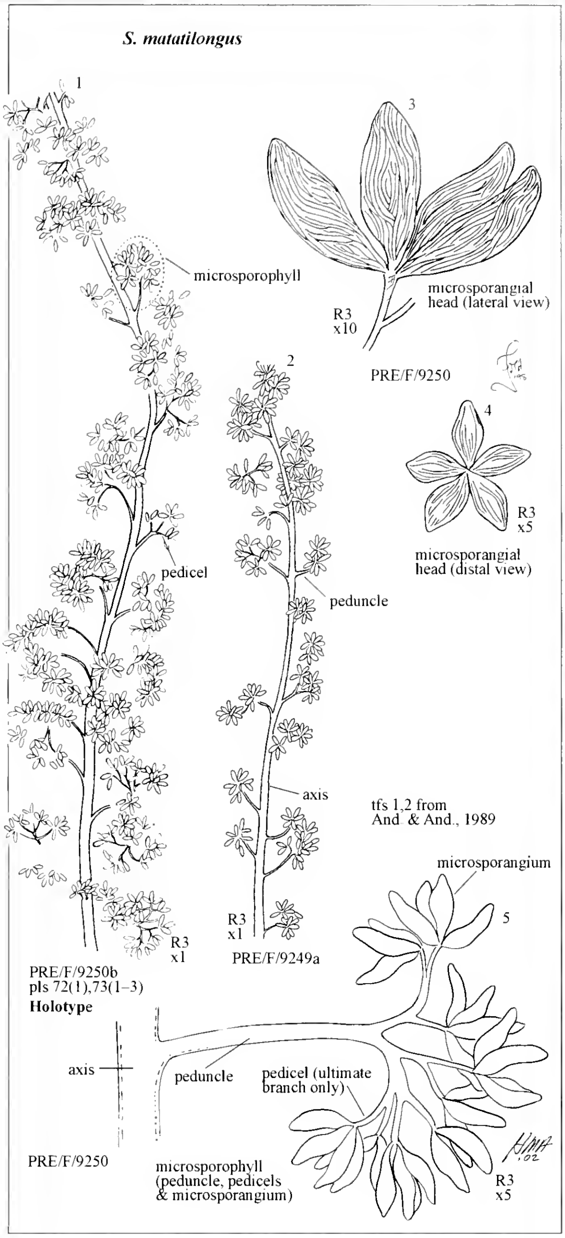
Sister palaeodemes—1 only (as listed)
San 111 Dic cra: 1 indiv. (intact).

Specific diagnosis
A *Stachyopitys* species with long, linear strobili, bearing simple to multi-branched microsporophylls with narrowly elliptical microsporangia.

Diagnostic characters
Attachment: unknown.
Strobilus: linear, long (up to >140 x 20 mm).
Microsporophyll: peduncles simple to forked to multiple-branched.
Fertile head: ultimate heads with 3 or 4 microsporangia.
Microsporangium: narrowly sinuously elliptical.

Etymology
matatilongus—referring to the long strobilus from the Matatiele locality.

Comment & comparison
With its long spicate strobili, *S. matatilongus* is by far the most impressive and distinctive of the *Stachyopitys* species.



Stachyopitys matatiramus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: BP/2/3115; pl. 74(5, 7).
Assemblage (TC): Mat 111 Dic dub, Matatiele.
Preservation: intact strobilus, base missing, no counterpart; impression, in thickly laminated, olive-grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 16 indivs (11 intact, 5 partial), pl. 74(1–13).

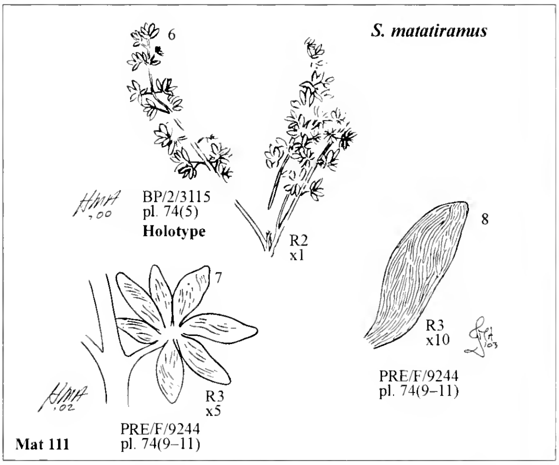
Sister palaeodemes—1 only (as listed)
Tel 111 Hei elo: 1 indiv. (partial).

Specific diagnosis
A *Stachyopitys* species with small compound (fasciculate) strobili, bearing simple microsporophylls with narrowly elliptical microsporangia.

Diagnostic characters
Attachment: with up to 4 strobili arising from a linear short shoot.
Strobilus: linear, spicate, relatively small (to 40 x 7 mm).
Microsporophyll: peduncles almost exclusively simple.
Fertile head: with *ca* 4 to 7 microsporangia.
Microsporangium: narrowly sinuously elliptical.

Etymology
matatiramus—*matati*, for the type locality; *ramus* (Lat.), branch, referring to the branched structure.

Comment & comparison
S. matatiramus occurs in the same TC (Mat 111) as *S. matatilongus* and is distinguished by its far smaller size and the branched structure of the strobilus. The species is reminiscent of *Antevsia mazenodensis* (affiliate of *Peltaspermum*) which, however, has sessile microsporangial clusters (see p. 155).



Stachyopitys gypsianthus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/13074a,b; pl. 75(1, 2, 8).
Assemblage (TC): Aas 411 Dic/Sph, Aasvoëlberg.
Preservation: complete strobilus, part and counterpart; impression, in thinly laminated, strongly baked, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for the holotype.
Specimens: 44 indivs (21 intact, 23 fragm.), pl. 75(1–9).

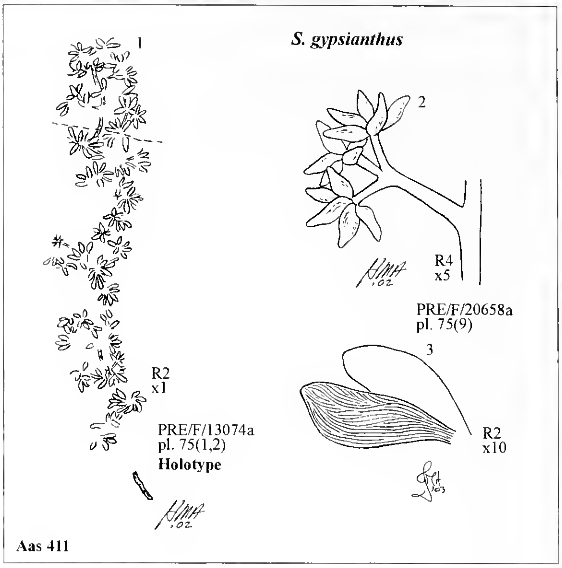
Sister palaeodeme—2 (best 1 listed)
Lut 111 Hei/Dic: 10 indivs (1 intact, 8 partial, 1 isolated).

Specific diagnosis
A *Stachyopitys* species with medium-sized linear strobili, bearing simply branched microsporophylls with narrowly elliptical microsporangia.

Specific characters
Attachment: unknown.
Strobilus: linear, spicate, of medium size (up to *ca* 60 x 12 mm).
Microsporophyll: peduncles branching distally.
Fertile head: ultimate heads with *ca* 3–6 microsporangia.
Microsporangium: narrowly sinuously elliptical.

Etymology
gypsianthus—*gyps* (Gr.), vulture, with reference to the type locality, Aasvoëlberg (Afrikaans), meaning 'vulture mountain'; *anthos*, flower.

Comment & comparison
S. gypsianthus is most like *S. matatilongus* from Mat 111, but differs in the strobili being consistently shorter, smaller and the pedicels not having multiple branching. It differs from the somewhat similar *S. matatiramus* in bearing simply branched microsporophylls.



Stachyopitys lacrisporangia J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: BP/2/5073a,b; pl. 77(1–5).
Assemblage (TC): Bir 111 Sph 2spp, Birds River.
Preservation: complete strobilus attached to bulbous base, part and counterpart; impression, in thinly laminated, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for the holotype.
Specimens: robust group—53 indivs (38 intact, 11 partial, 4 isolated), slender group—57 indivs (44 intact, 10 fragm., 3 isolated), pls 76, 77.

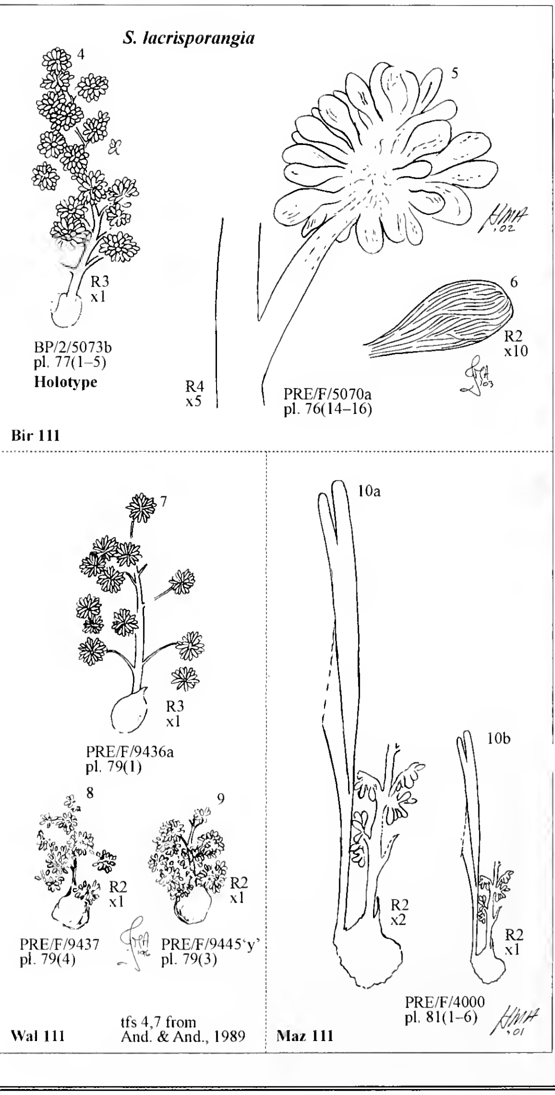
Sister palaeodemes—22 (best 2 listed)
Tel 111 Hei elo: 44 indivs (21 intact, 16 fragm., 7 isolated), pl. 78(1–12).
Wal 111 Dic odo: 20 indivs (8 intact, 8 partial, 4 isolated), pl. 78(1–4).

Specific diagnosis
A *Stachyopitys* species with short, linear to broadly spicate strobili, bearing simple microsporophylls with clavate or tear-shaped microsporangia.

Specific characters (based on reference palaeodeme, Bir 111)
Attachment: with a single strobilus attached to a bulbous short shoot.
Strobilus: linearly to broadly spicate, relatively small (up to *ca* 40 x 12 mm).
Microsporophyll: peduncles simple.
Fertile head: with numerous (up to >20) microsporangia.
Microsporangium: clavate or tear-shaped.

Etymology
lacrisporangia—*lacrima* (Lat.), tear, referring to the tear-shaped microsporangia.

Comment & comparison
This is the most frequent and abundant of the *Stachyopitys* species occurring in the Molteno. The many palaeodemes show a wide range of variation, but at present we find no justification for distinguishing further species within the group. Two forms with the robust and the slender axes are separated out in Tab. 50. At Bir 111, about equal numbers of specimens occur in these two groups. The holotype derives from the more robust category.
The attached specimen from Maz 111 (tf. 10 adjacent) is regarded as belonging to *S. lacrisporangia*.



Stachyopitys rotundisporangia J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: BP/2/5072; pl. 79(5–9).
Assemblage (TC): Bir 111 Sph 2spp, Birds River.
Preservation: complete strobilus attached to bulbous base, without counterpart; impression, in thinly laminated, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 3 indivs (2 intact, 1 fragm.); pl. 79(5–9).

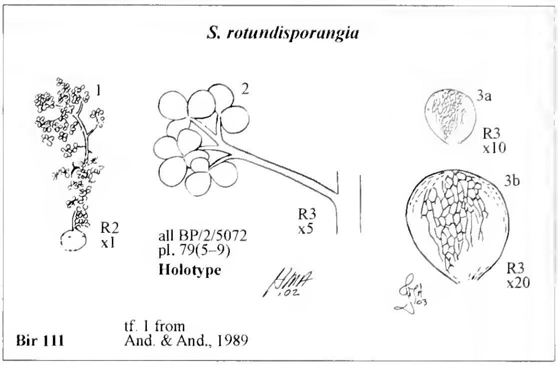
Sister palaeodemes—1 only (as listed)
Aas 411 Dic/Sph: 7 indivs (3 intact, 3 partial, 1 isolated).

Specific diagnosis
A *Stachyopitys* species with small, broadly spicate strobili, bearing simply branched microsporophylls with spherical microsporangia.

Specific characters (based on reference palaeodeme, Bir 111).
Attachment: with a single strobilus attached to a bulbous short shoot.
Strobilus: broadly spicate, small (up to *ca* 27 x 11 mm).
Microsporophyll: peduncles branching distally.
Fertile head: ultimate heads with *ca* 3 or 4 microsporangia.
Microsporangium: spherical.

Etymology
rotundisporangia—*rotundus* (Lat.), almost circular, rounded, referring to the spherical microsporangia.

Comment & comparison
The reference palaeodeme of this species is represented by the holotype (a clearly preserved complete specimen) and only two further individuals. It differs from other *Stachyopitys* species in the small spherical microsporangia.



Stachyopitys maziramus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/4652; pl. 80(1, 2).
Assemblage (TC): Maz 211 Hei/Dic, Mazenod.
Preservation: complete strobilus attached to bulbous base, without counterpart; compression, in thinly laminated, carbonaceous (poor cuticle), medium grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimen: holotype only.

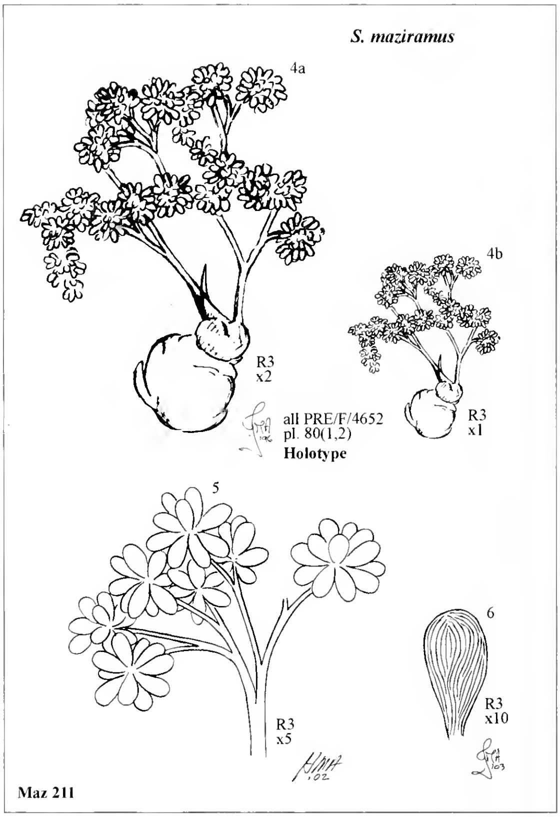
Sister palaeodemes—nil.

Specific diagnosis
A *Stachyopitys* species with short compound (fasciculate) strobili, bearing multibranched microsporophylls with ovate-elliptical microsporangia.

Specific characters (based on reference palaeodeme, Maz 211).
Attachment: with 2 or more strobili arising from a bulbous short shoot.
Strobilus: short, fasciculate (*ca* 12 x 12 mm).
Microsporophyll: peduncles variously multibranched.
Fertile head: ultimate heads with many (up to >15) microsporangia.
Microsporangium: ovate-elliptical.

Etymology
maziramus—*mazi*, for the type locality, Mazenod; *ramus* (Lat.), branch, referring to the branched structure of the strobilus.

Comment & comparison
S. maziramus, represented only by the holotype, is the rarest member of the genus. It differs from other *Stachyopitys* species in its compound multibranched axes. The 25 additional specimens of the genus from the Maz 211 TC are clearly different and fall in the robust form of *S. lacrisporangia*.



Sphenobaiera Florin 1936

Type species
Sphenobaiera spectabilis (Nath. 1906) Florin 1936.
Stabbarp, Scania, Sweden; Liassic, Jurassic.

Generic concept
A ginkgoopsid leaf with indistinct petiole, deeply dichotomously dividing wedge-shaped lamina and forking subparallel venation.

Generic characters (Molteno Fm.)
Attachment: leaves fascicled or in a close spiral at the end of short shoots.
Leaf: linear to broadly wedge-shaped with margins diverging at <90°, lamina simple to deeply dichotomously dividing, with each segment to several times forked; petiole not distinct; veins subparallel, repeatedly forking, relatively well spaced, converging distally to end separately at segment apex.
Cuticle: see And. & And. (1989, p. 133); this vol., tfs 1–4 below.

Etymology
Sphenobaiera—*spheno* (Gr.) wedge; *Baiera*, a genus for ginkgoopsid leaves.

Global range: numerous species, Pangaea, P.–U.K.

Gondwana Triassic occurrence (after And. & And. 1989)
Frequency (F): 26 degree squares (of the 84 across Gondwana).
Ubiquity (U): 5 continents (of 5 comprising Gondwana).
Diversity (D): 12 foliage species.
Abundance (A): 30% (the norm in Molteno TCs).
Longevity (L): 26 myrs (Spathian to later Norian).

Colonisation success: FUDAL rating 26/5/12/30/26 = 99.
High success (Grade 4); *Sphenobaiera* was the third most prominent genus in the Gondwana Triassic; it was frequent, ubiquitous, diverse, abundant and long-lived.
Endemism: of the 12 Gondwana Triassic species, six occur more or less widely through the realm, one is a basin endemic and five are single-assemblage endemics.

Molteno occurrence
Frequency (F): 43 TCs (of 100 sampled in the Molteno).
Diversity (D): 9 species.
Abundance (A): monodominant (>70%) in 7 TCs; co-dominant (20–69%) in 7 TCs; abundant to occasional (1–19%) in 9 TCs; rare to very rare (<1%) in 20 TCs.

Habit: probably woody shrubs to large trees.
Preferred habitat: *Sphenobaiera* is the monodominant or co-dominant taxon in lake deposit TCs. It is relatively rare elsewhere.

Affiliated organs
Female strobilus: *Hamshawvia*—Grade 4/5 (Org. att., Cut. cor., Mut. occ., Kin. reinf.).
Male strobilus: *Stachyopitys*—Grade 5 (Org. att., Mut. occ.).
See relevant text under *Hamshawvia* and *Stachyopitys*. Both these genera have been found in organic connection with *Sphenobaiera* leaves, but for reasons previously outlined, a Grade 4/5 affiliation is given for *Hamshawvia*. Slender stems with irregularly spiralled leafless short shoots (much like in extant *Ginkgo*) occur in some *Sphenobaiera* woodland TCs (e.g. Bir 111 and Aas 411). It is likely that these originally bore *Sphenobaiera* foliage.

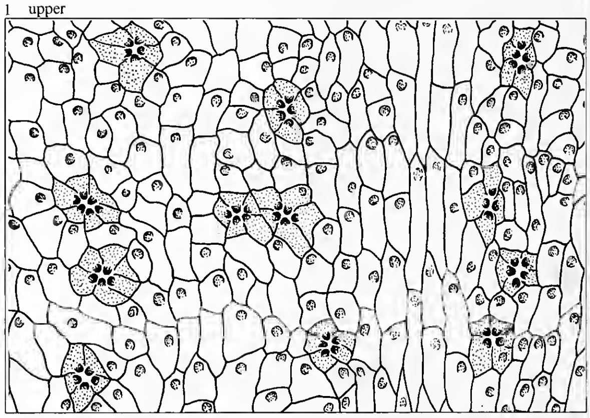
Classification & comparison
Intergeneric comparisons
Gondwana Triassic—In gross leaf morphology, notably the dichotomising nature of both lamina and venation, *Sphenobaiera* and *Ginkgoites* are clearly alike. Certain linear-leaved forms of *Sphenobaiera* and *Dicroidium* (i.e. *S. pontifolia* and *D. elongatum* subsp. *argentinum*) do, however, prove virtually indistinguishable other than through examination of their cuticles.

Other ginkgoalean genera—The twelve species of *Sphenobaiera* from the Gondwana Triassic conform in the main to the concept of the genus, but in several instances and in certain features, transgress (or approach very closely) the boundaries of adjacent ginkgoalean or czekanowskialean genera. Such genera include *Baiera*, *Pseudotorellia*, *Eretmophyllum*, *Czekanowskia* and *Phoenicopsis*.

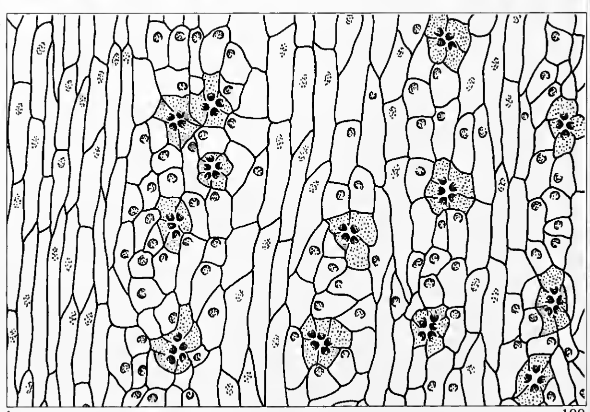
Other genera—The lanceolate undivided forms of *Sphenobaiera* (*S. insecta* and *S. calensis*) are superficially very like the Gondwana Triassic conifer *Heidiphyllum*, but are readily separated on the basis of cuticle and the absence of interveinal striae.

Interspecific comparisons
As is generally the case, diversity in the Molteno is more readily recognised in the foliage (*Sphenobaiera*, nine species) than in the female (*Hamshawvia*, four species) and male (*Stachyopitys*, six species) affiliates. Many of the Molteno palaeodemes of *Sphenobaiera*, as in *Dicroidium*, are complex and bridge two or more of the defined species. Again, like *Dicroidium*, *Sphenobaiera* actively colonised and diversified through much of the Triassic, with hybridisation and polyploidy probably widespread—suggesting a reticulate rather than punctuate evolutionary model. For a full systematic coverage of the nine Molteno species, with comprehensive photographic cover and line drawings of palaeodemes, refer to And. & And. (1989, pp. 130–217).

1 upper



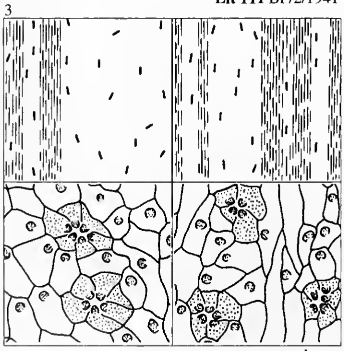
2



lower x100

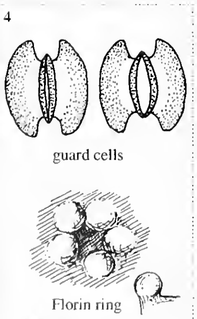
Sphenobaiera schenckii
Lit 111 BP/2/1941

3

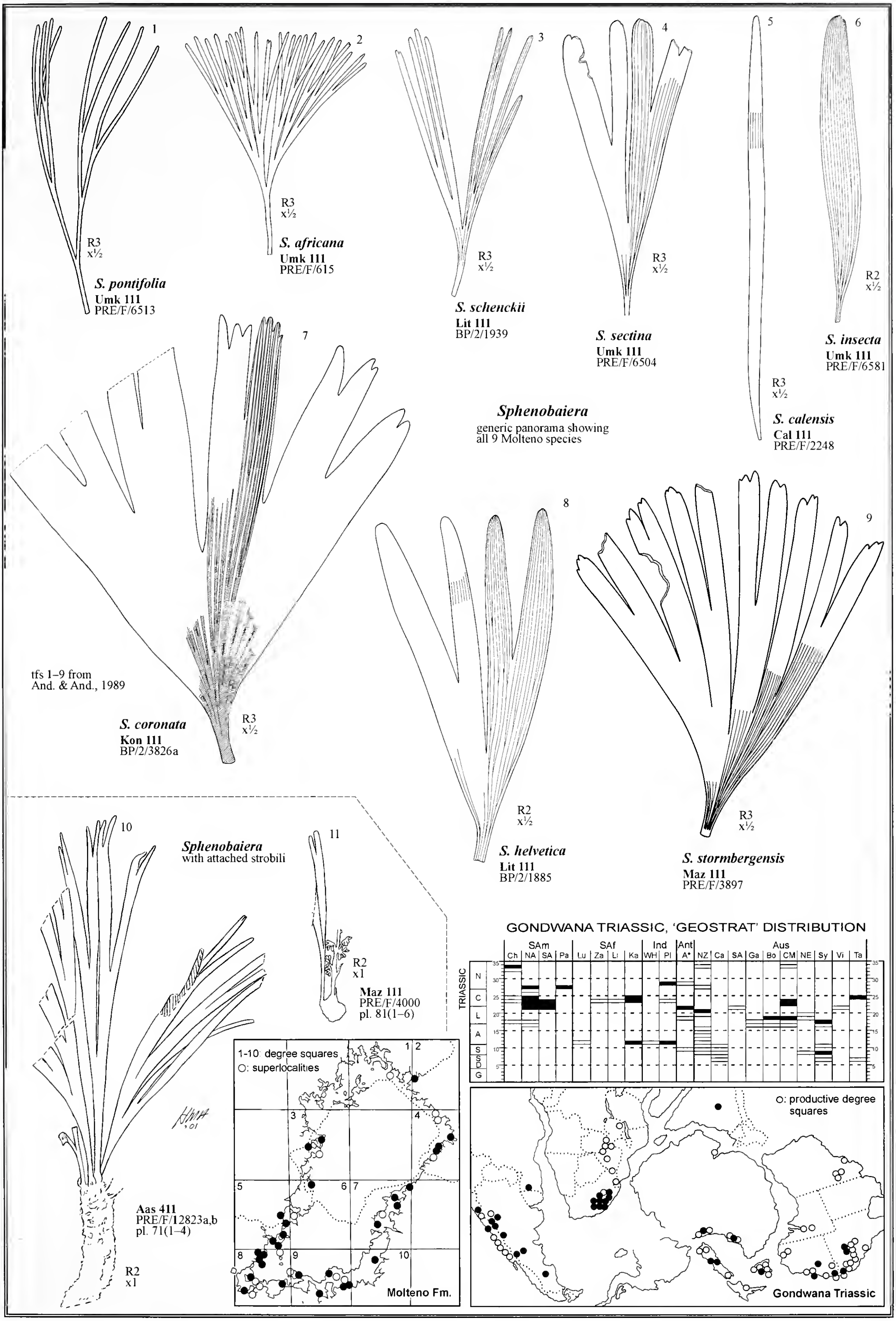


upper lower

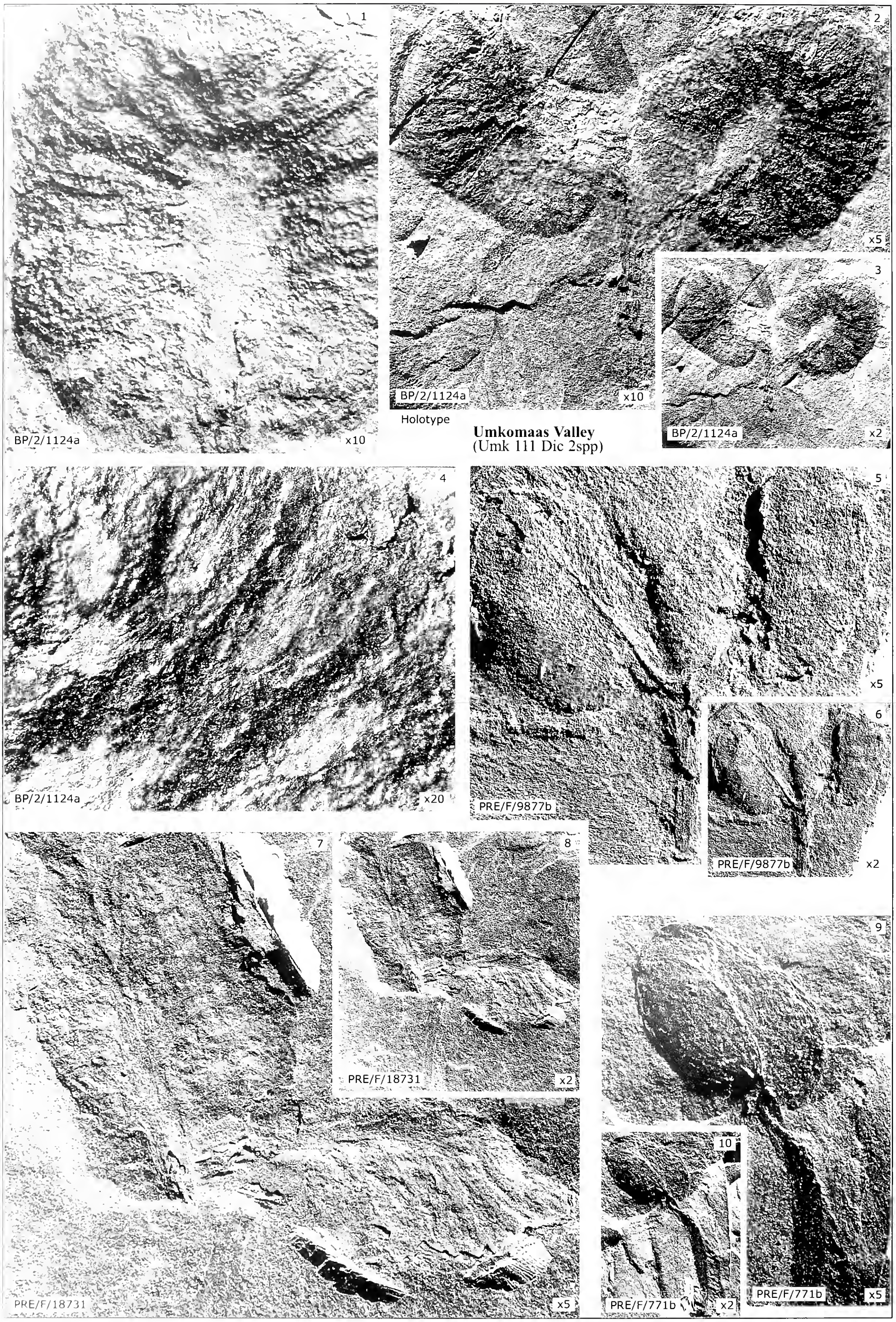
4

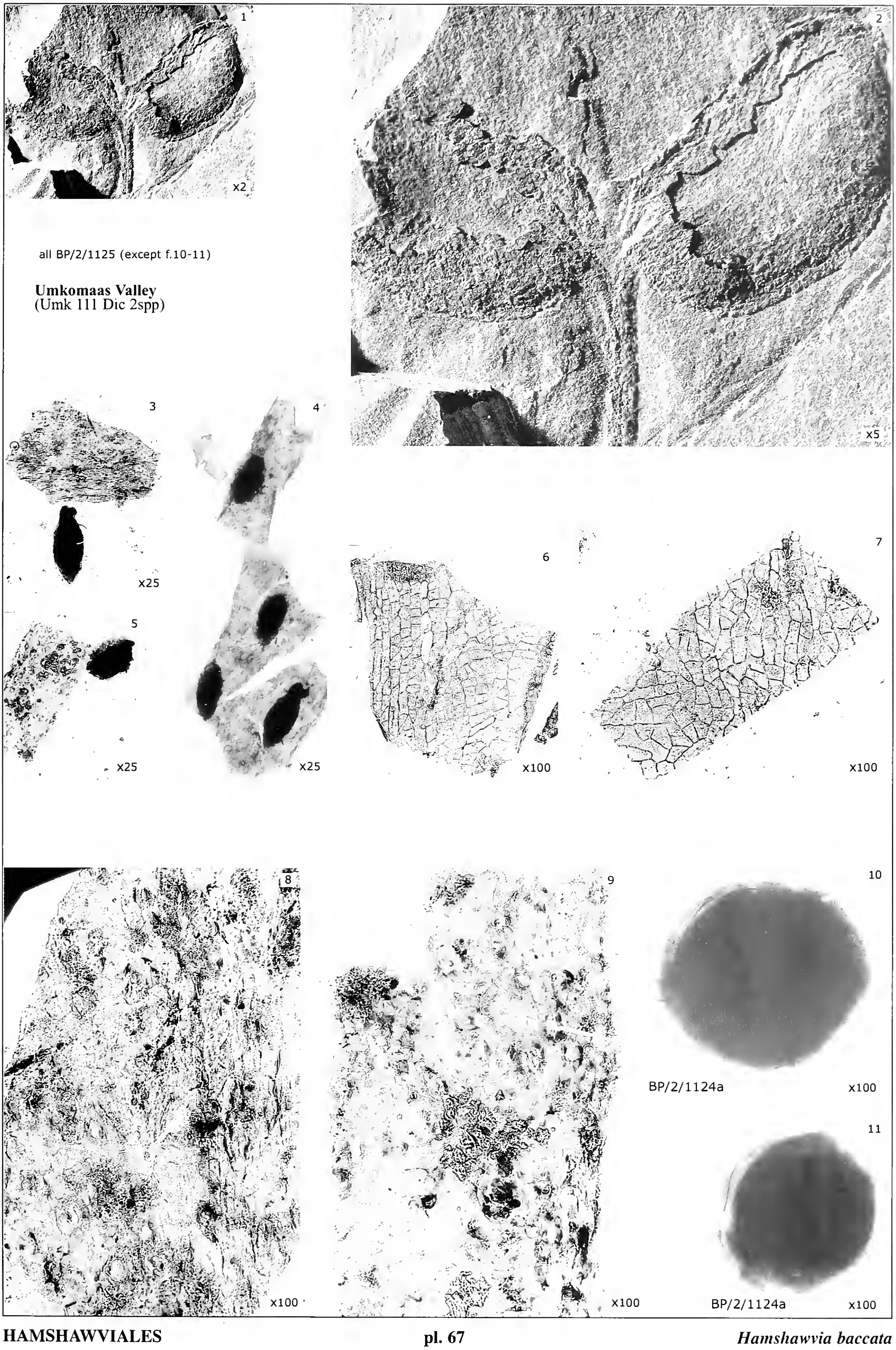


x500

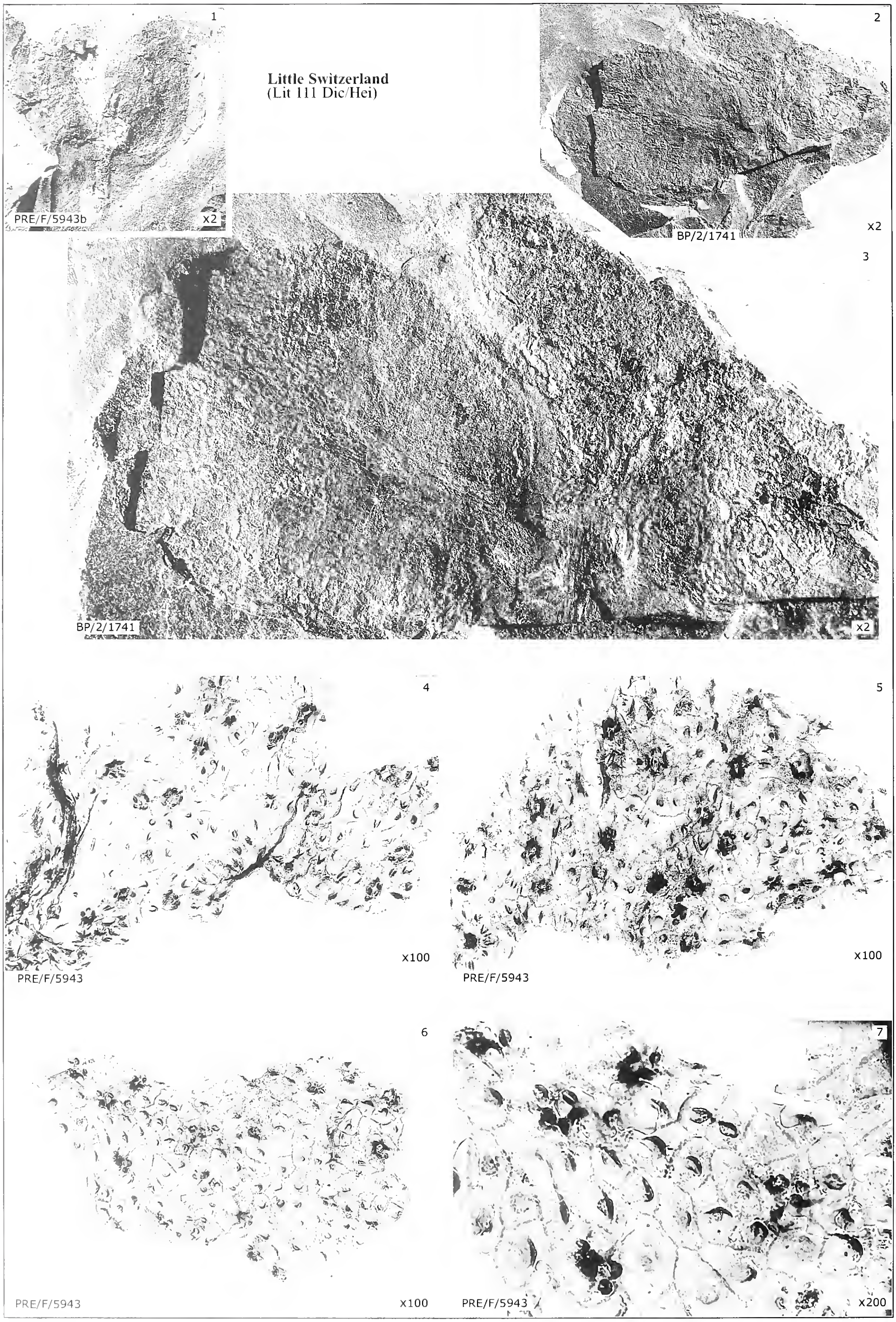


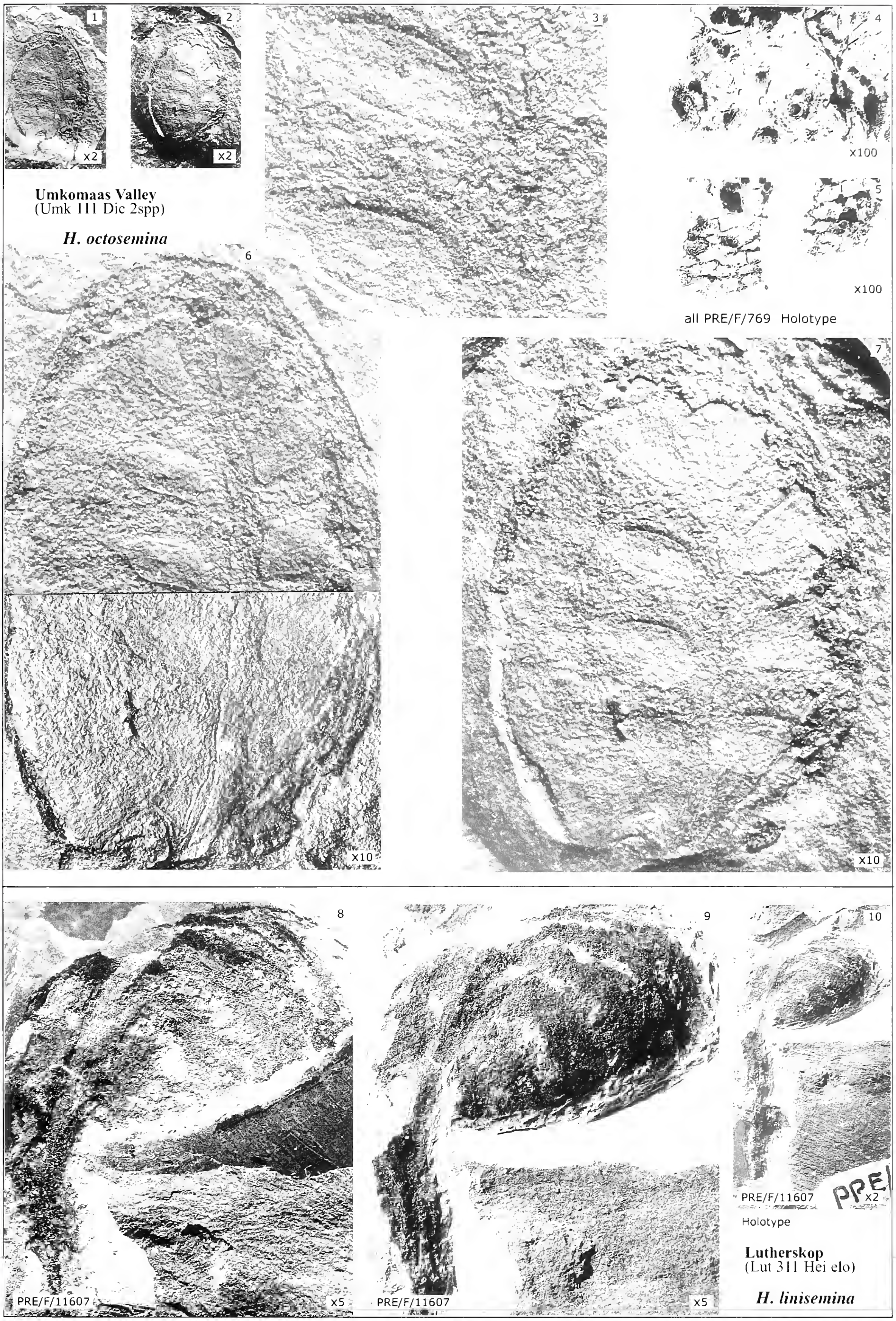
1
R3
x½
S. pontifolia
Umk 111
PRE/F/6513
2
R3
x½
S. africana
Umk 111
PRE/F/615
3
R3
x½
S. schenckii
Lit 111
BP/2/1939
4
R3
x½
S. sectina
Umk 111
PRE/F/6504
5
R3
x½
S. calensis
Cal 111
PRE/F/2248
6
R2
x½
S. insecta
Umk 111
PRE/F/6581
Sphenobaiera
generic panorama showing
all 9 Molteno species
7
tfs 1–9 from
And. & And., 1989
S. coronata
Kon 111
BP/2/3826a
R3
x½
8
R2
x½
S. helvetica
Lit 111
BP/2/1885
9
R3
x½
S. stormbergensis
Maz 111
PRE/F/3897
10
Sphenobaiera
with attached strobili
11
R2
x1
Maz 111
PRE/F/4000
pl. 81(1–6)
Aas 411
PRE/F/12823a,b
pl. 71(1–4)
R2
x1
GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION
SAm
SAf
Ind
Ant
Aus
Ch
NA
SA
Pa
Lu
Za
Li
Ka
WH
Pl
A*
NZ
Ca
SA
Ga
Bo
CM
NE
Sy
Vi
Ta
TRIASSIC
N
C
L
A
S
G
1-10: degree squares
○: superlocalities
Molteno Fm.
○: productive degree squares
Gondwana Triassic


1
BP/2/1124a
x10
2
x5
BP/2/1124a
x10
Holotype
3
BP/2/1124a
x2
Umkomaas Valley
(Umk 111 Dic 2spp)
4
BP/2/1124a
x20
5
x5
PRE/F/9877b
6
PRE/F/9877b
x2
7
PRE/F/18731
x5
8
PRE/F/18731
x2
9
PRE/F/771b
x5
10
PRE/F/771b
x2

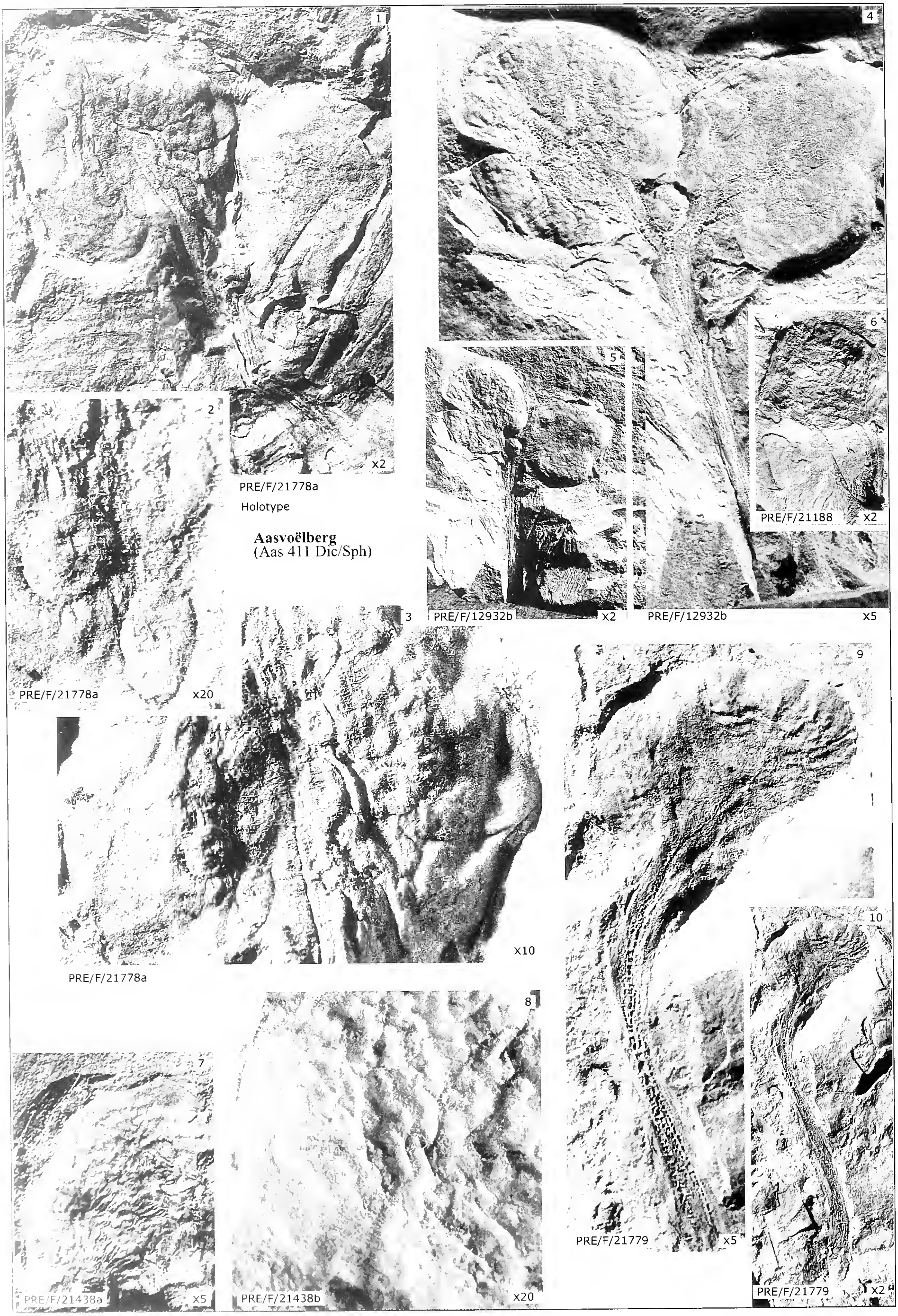


HAMSHAWVIALES **pl. 67** ***Hamshawvia baccata***

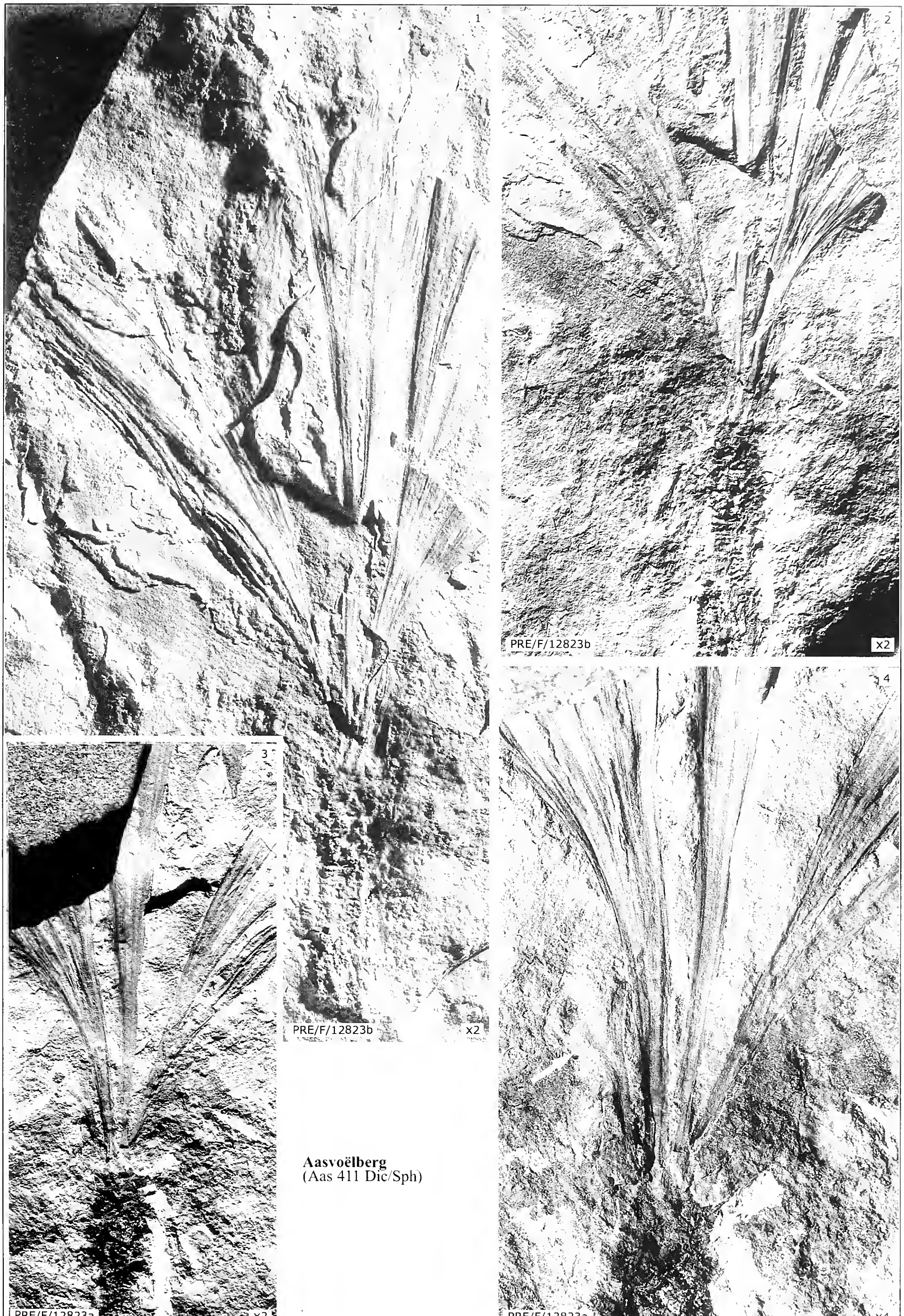

Little Switzerland
(Lit 111 Dic/Hei)
1
PRE/F/5943b
x2
2
BP/2/1741
x2
3
BP/2/1741
x2
4
x100
PRE/F/5943
5
x100
PRE/F/5943
6
PRE/F/5943
x100
7
PRE/F/5943
x200



HAMSHAWVIALES **pl. 69** ***Hamshawvia* spp.**



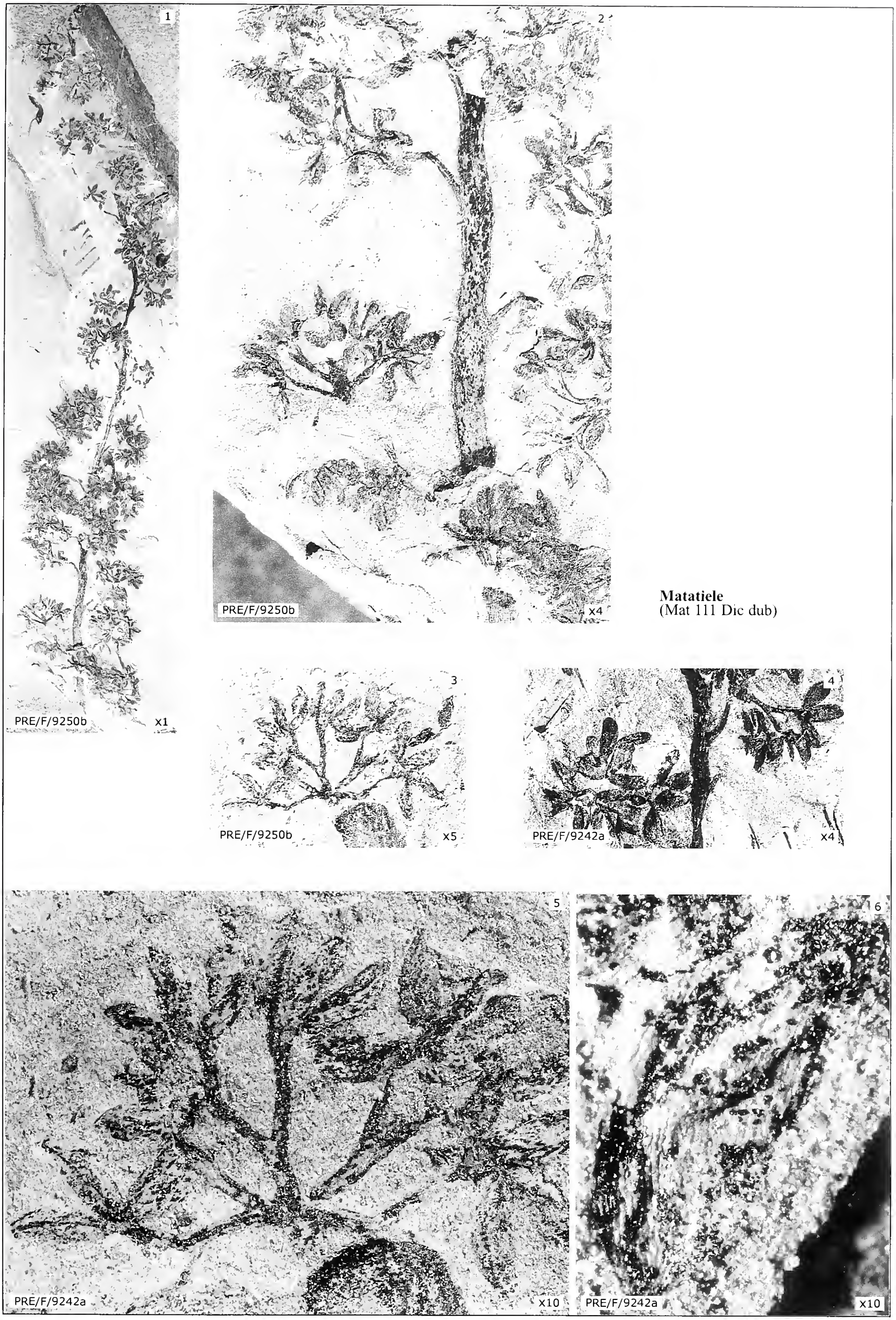
Hamshawvia longipedunculata **pl. 70** **HAMSHAWVIALES**



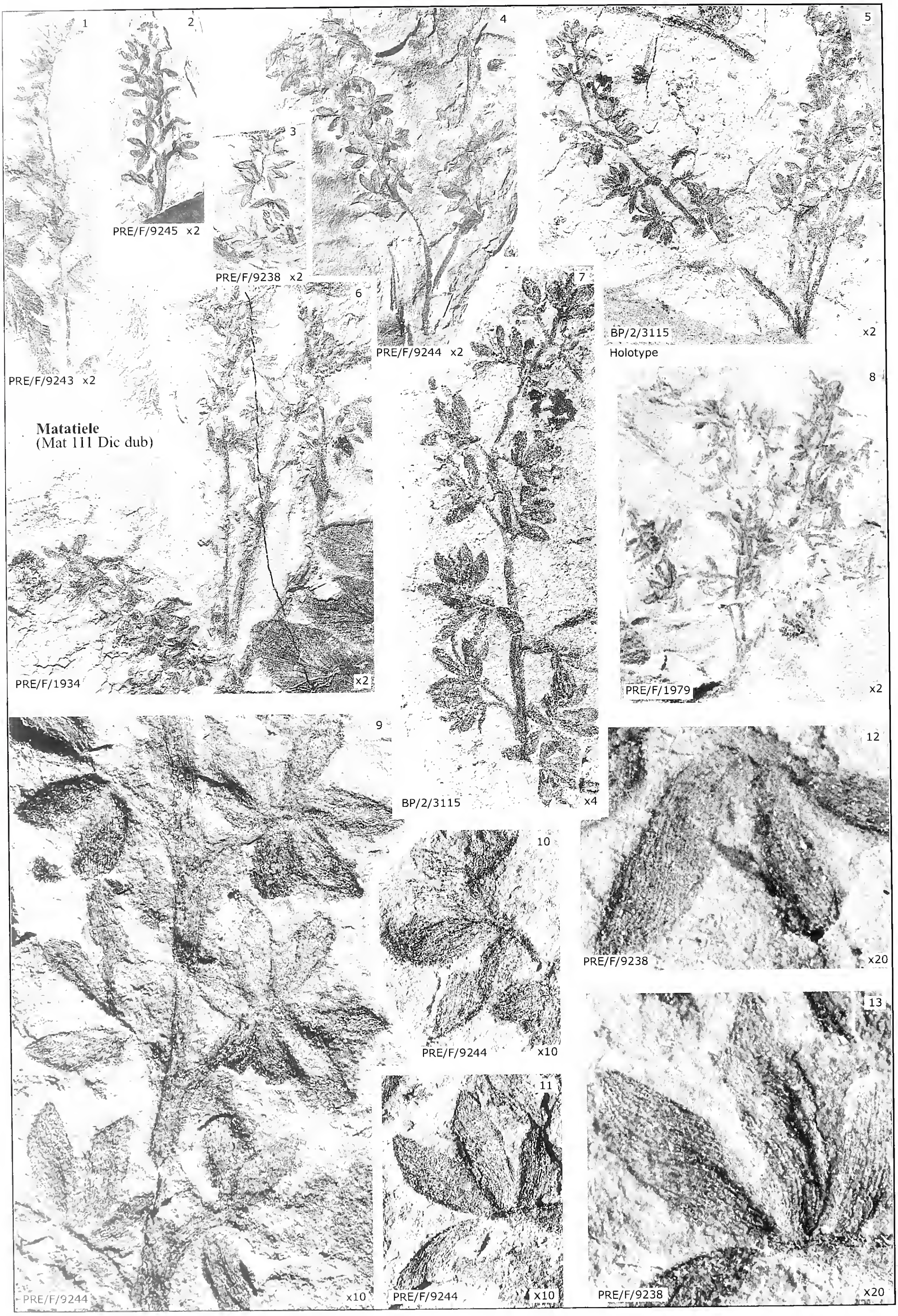
Aasvoëlberg
(Aas 411 Dic/Sph)

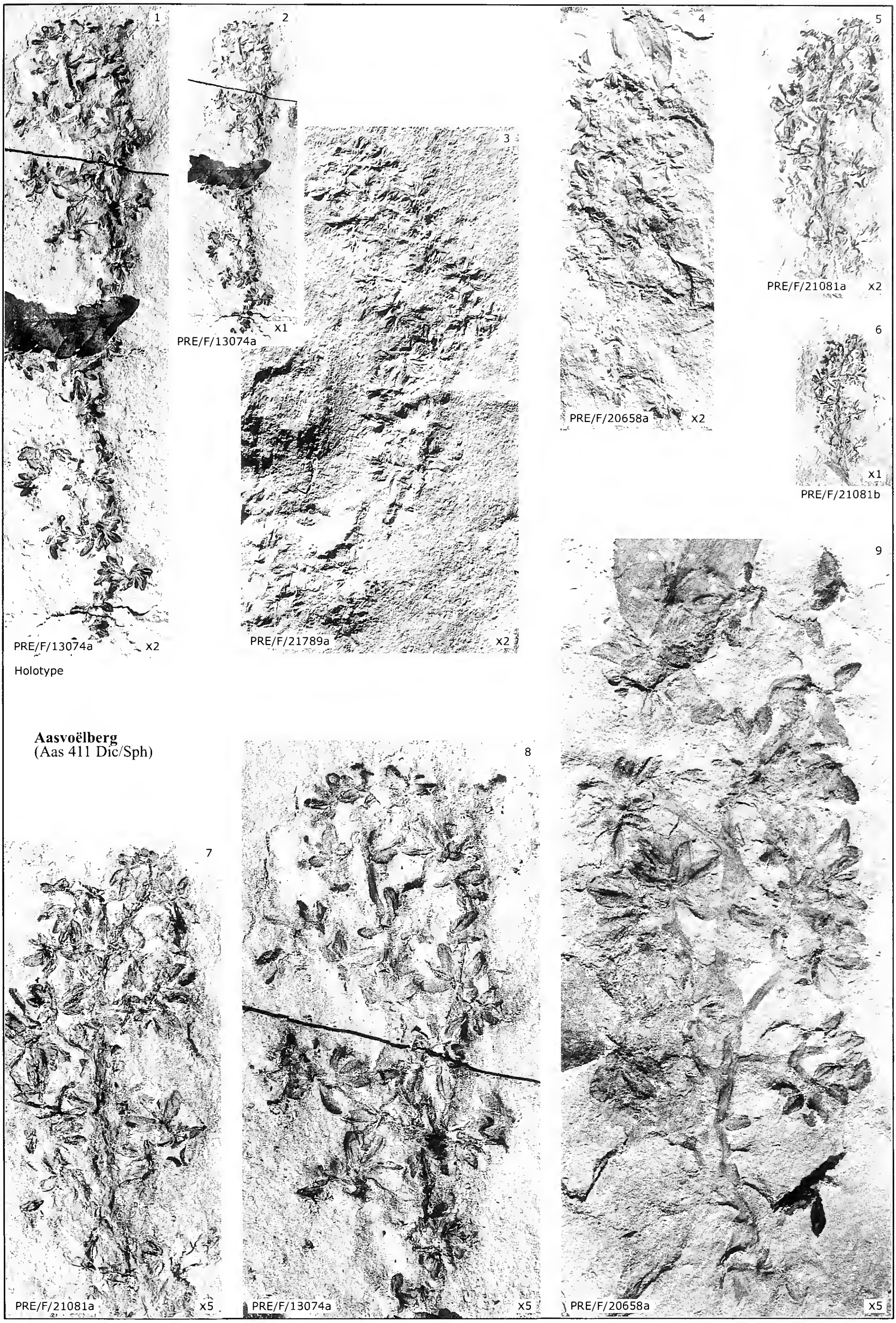
HAMSHAWVIALES **pl. 71** ***Hamshawvia/Sphenobaiera***

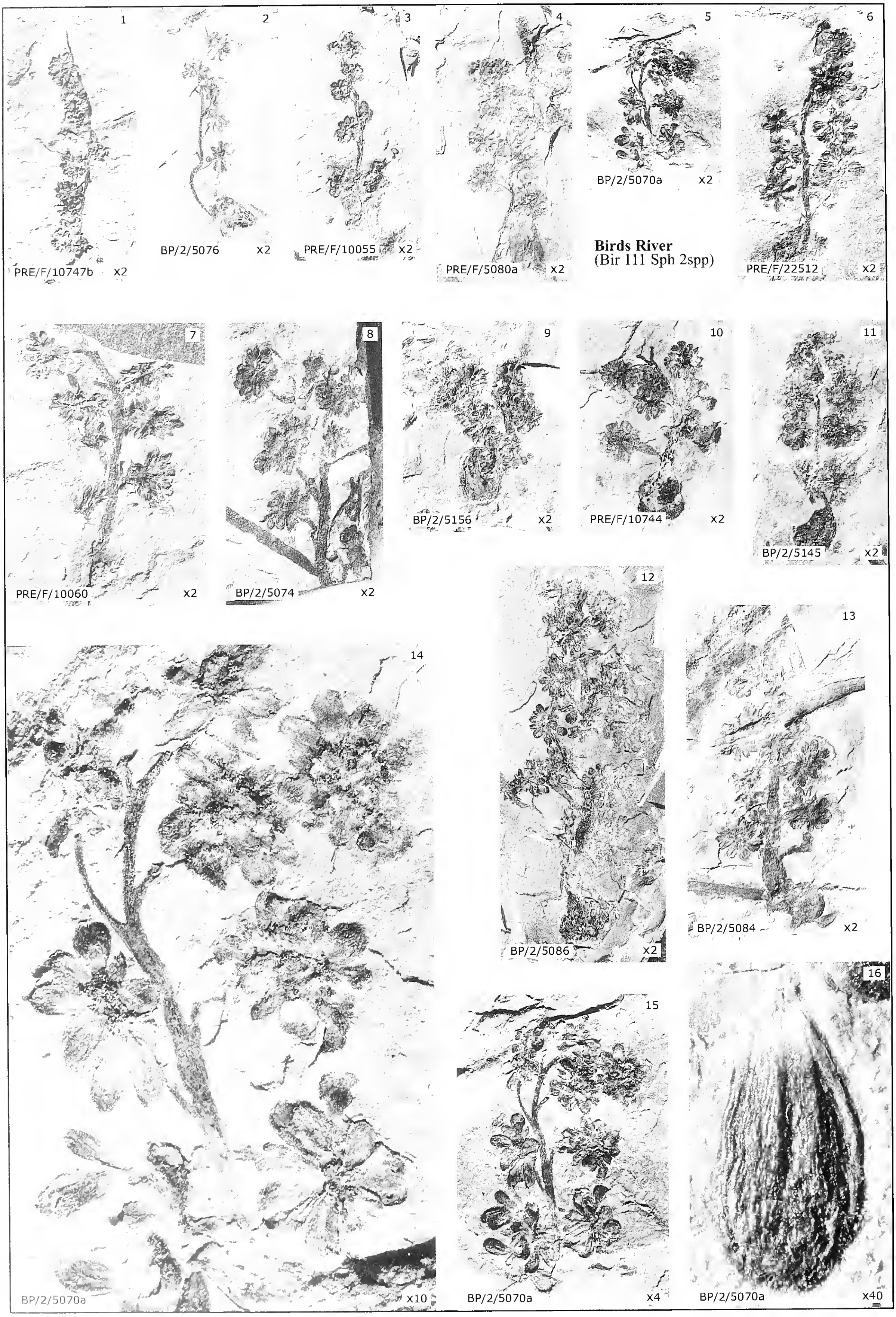
Matatiele
(Mat 111 Dic dub)



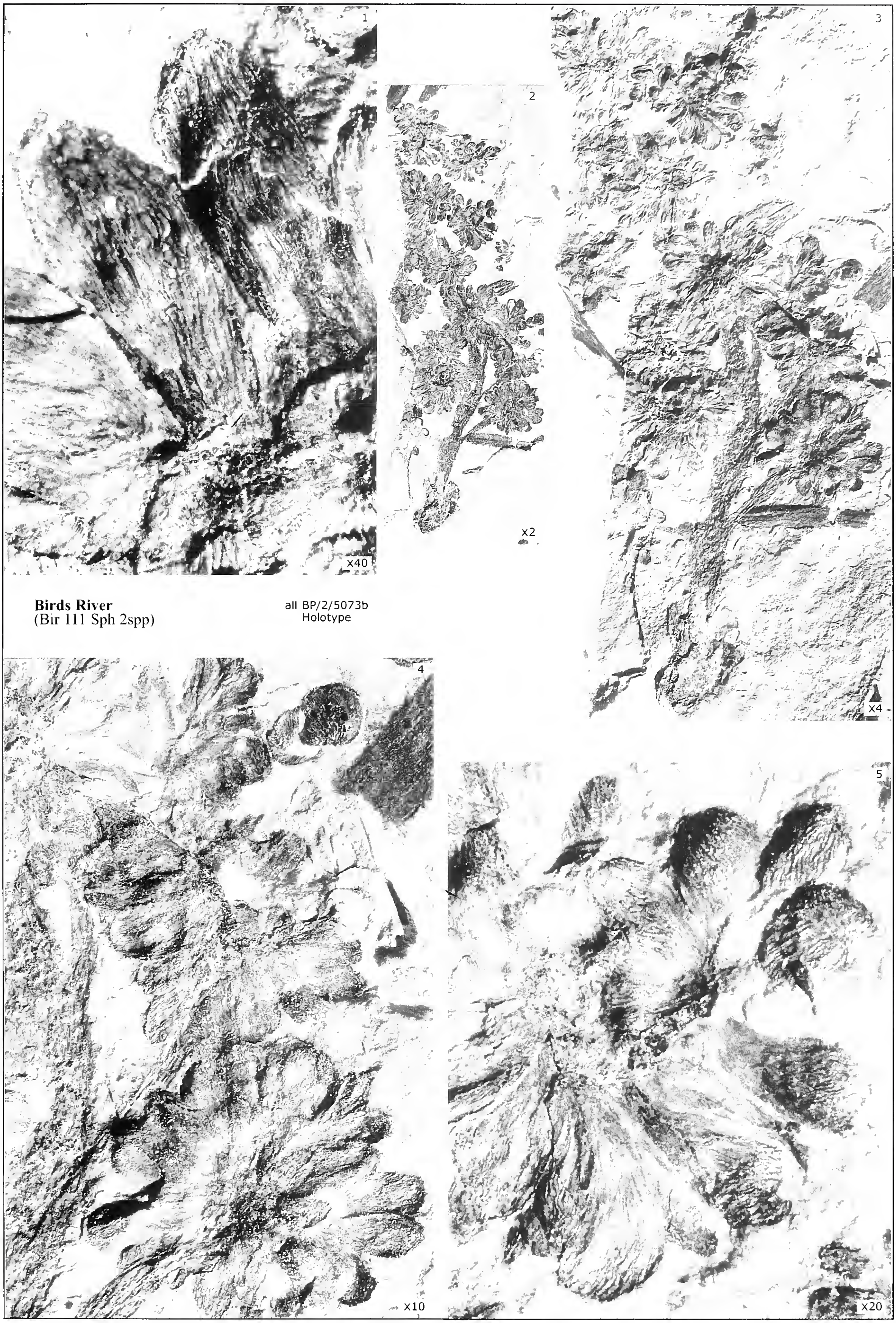
Matatiele
(Mat 111 Dic dub)


1
2
3
4
5
PRE/F/9245 x2
PRE/F/9238 x2
PRE/F/9244 x2
BP/2/3115
Holotype
x2
PRE/F/9243 x2
6
7
8
Matatiele
(Mat 111 Dic dub)
PRE/F/1934
x2
PRE/F/1979
x2
9
BP/2/3115
x4
12
10
PRE/F/9238
x20
PRE/F/9244
x10
11
13
PRE/F/9244
x10
PRE/F/9244
x10
PRE/F/9238
x20


1
PRE/F/13074a x2
Holotype
2
PRE/F/13074a x1
3
PRE/F/21789a x2
4
PRE/F/20658a x2
5
PRE/F/21081a x2
6
PRE/F/21081b x1
Aasvoëlberg
(Aas 411 Dic/Sph)
7
PRE/F/21081a x5
8
PRE/F/13074a x5
9
PRE/F/20658a x5

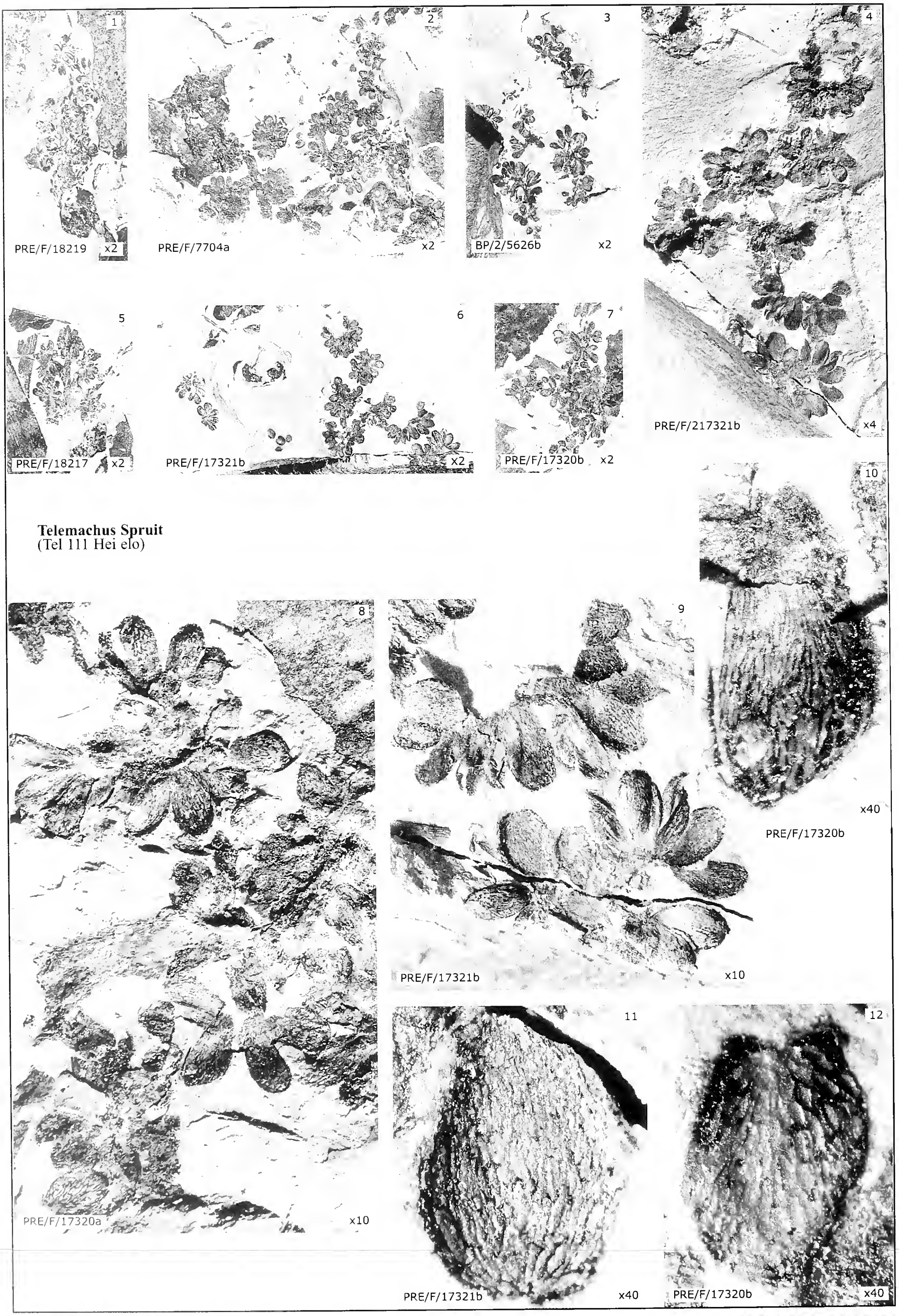


Stachyopitys lacrisporangia **pl. 76** **HAMSHAWVIALES**

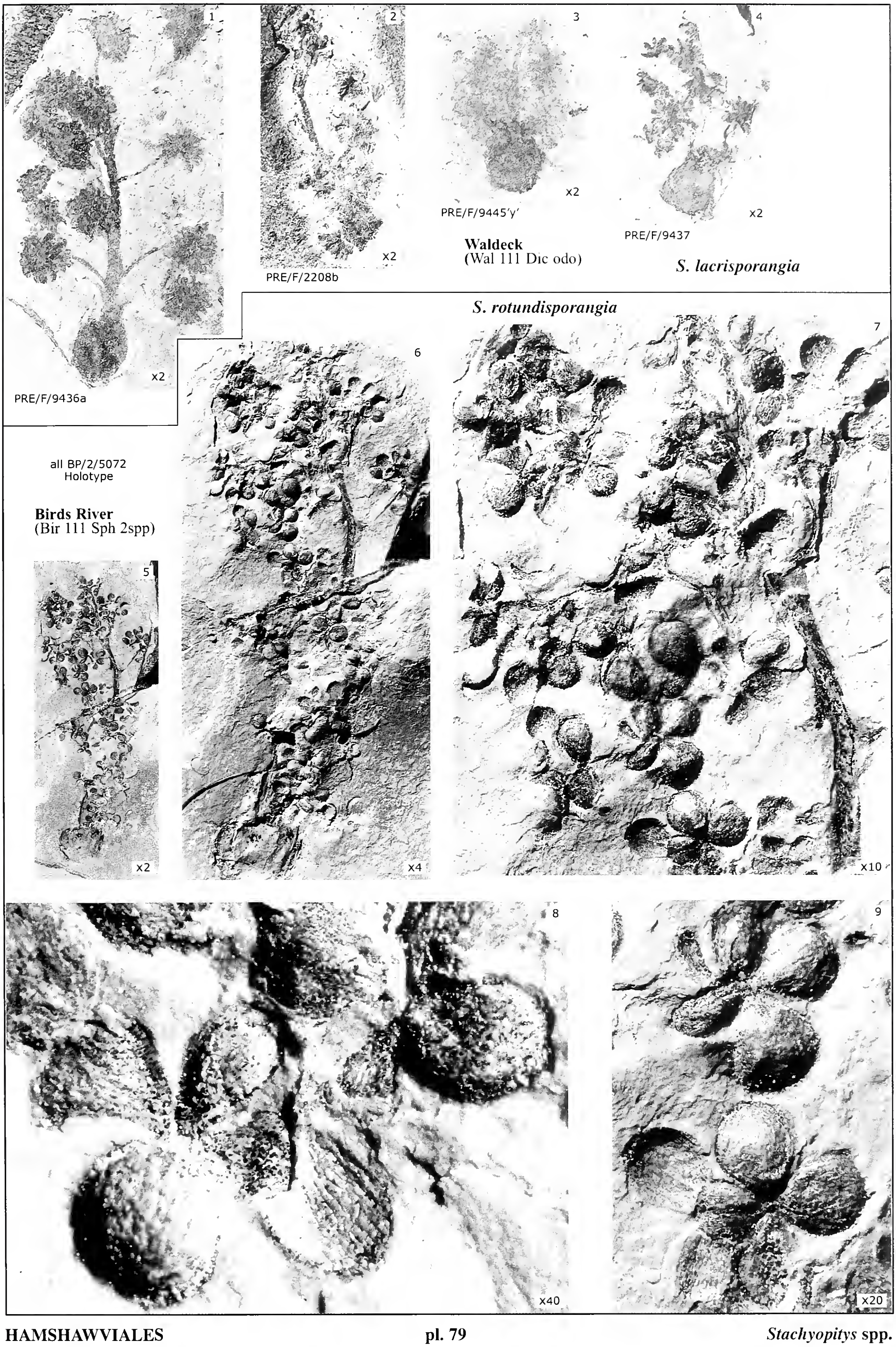


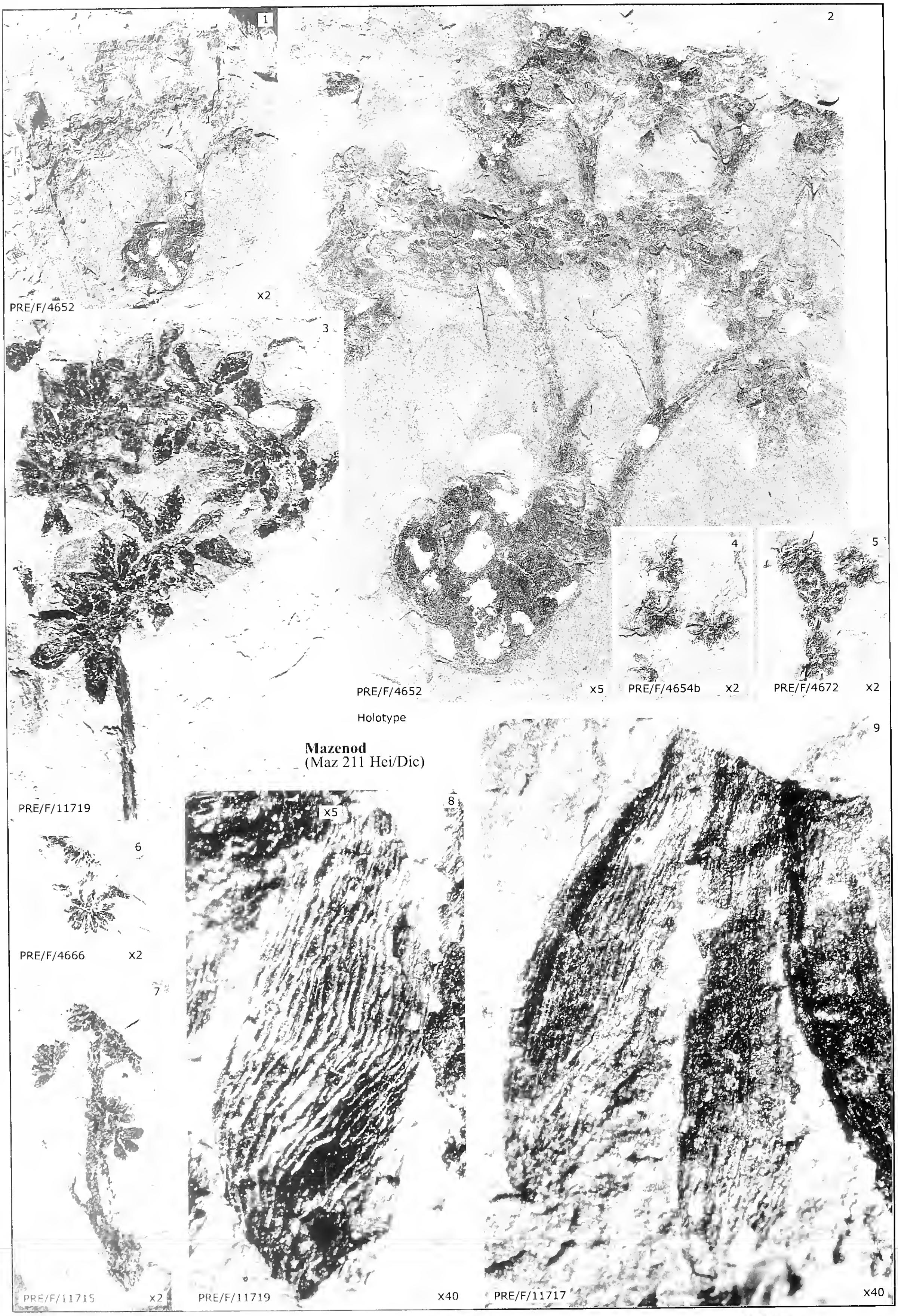
Birds River
(Bir 111 Sph 2spp)

all BP/2/5073b
Holotype

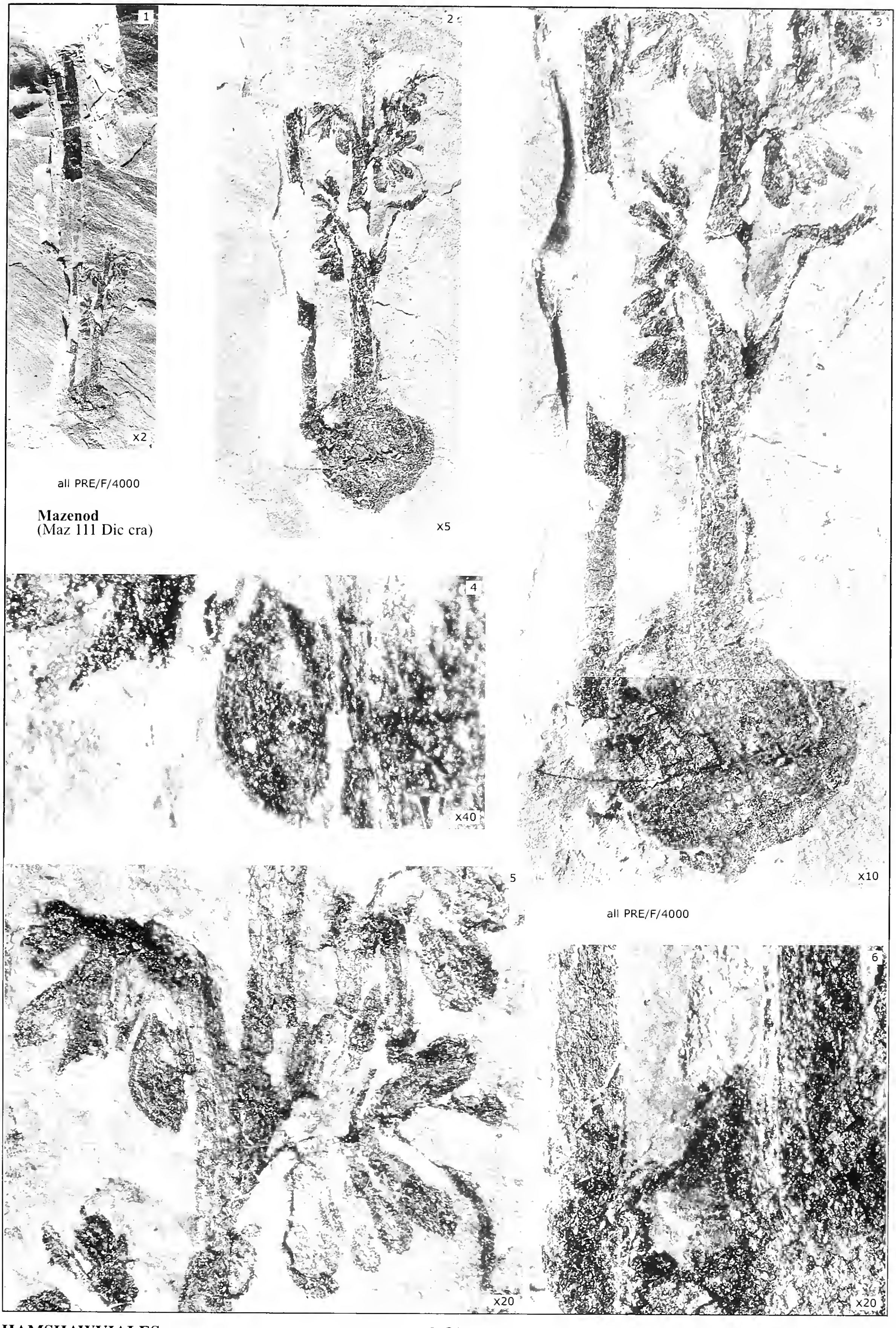


Stachyopitys lacrisporangia **pl. 78** **HAMSHAWVIALES**


1
x2
PRE/F/9436a
2
x2
PRE/F/2208b
3
x2
PRE/F/9445'y'
Waldeck
(Wal 111 Dic odo)
4
x2
PRE/F/9437
S. lacrisporangia
S. rotundisporangia
all BP/2/5072
Holotype
Birds River
(Bir 111 Sph 2spp)
5
x2
6
x4
7
x10
8
x40
9
x20



Stachyopitys maziramus pl. 80 HAMSHAWVIALES



HAMSHAWVIALES **pl. 81** ***Stachyopitys/Sphenobaiera***

GINKGOOPSIDA S.V.Meyen 1987
UMKOMASIALES S.V.Meyen 1984
UMKOMASIACEAE S.V.Meyen 1984

Umkomasia H.H.Thomas 1933

Synonyms
Pilophorosperma H.H.Thomas 1933 (see Holmes 1987).
Spermatocodon H.H.Thomas 1933.

Type species
Umkomasia macleanii H.H.Thomas 1933.
Umkomaas Valley, Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis emended
A ginkgoopsid strobilus of lax paniculate form with megasporophylls bearing 1–7 pairs of uni-ovulate cupules and seeds with bifid, curved micropyles.

Generic characters
Strobilus: simple, lax, paniculate, small to large (length 40–>150 mm); axis generally robust, erect, gradually tapering; megasporophylls several to many, attachment very variable, from semi-opposite or alternate, apparently planar to irregularly helical to irregularly decussate.
Megasporophyll: simple, pedunculate, planar to spicate; bracteoles prominent, singly or in opposite pairs, axillary or along peduncles; ovuliferous cupules recurved, pedicellate to sessile, in 1–7 opposite to subopposite pairs.
Cupule: small to large (3–20 mm deep), circular to roundly triangular to oval, partially flattened, uni-ovulate, fully to partially enclosing the ovule, generally deeply splitting at maturity into 2 or 4 regular lobes.
Ovule/seed: slightly asymmetrical, size and shape as per cupules, generally moderately platyspermic and weakly winged; micropyle pronounced, bifid, outwardly curved.

Etymology
Umkomasia—named by Thomas (1933) after the type locality.

Global range: several spp., Gondwana, Tr. (SCY–CRN)
First: *Umkomasia* sp. indet. (*Dicroidium* 'flowers'), White (1986), Clarence Siding, Banks Wall Fm., Blue Mts, Australia.
Last: *Umkomasia* sp. indet. (*Baiera tenuifolia*), Johnston (1888), Lord's Hill, Brady Fm., Hobart, Tasmania.

Gondwana Triassic occurrence
SAm—N. & S. Argentina, 3TCs (6 indivs).
SAf—Karoo Basin, 22 TCs (503 indivs).
Aus—Eastern Australia, 18 TCs (48 indivs); New Zealand 4 TCs (8 indivs).
Ant—Allan Nunatak, 1 TC (1 indiv.).

Molteno occurrence
Frequency (F): 22 TCs (of 100 sampled in the Molteno).
Diversity (D): 8 species.
Abundance (A): 503 indivs total; rare to very rare in top 8 TCs.

Mat 111 Dic dub:	>75 indivs in	65 man-hrs	(12 per 1 man-day)	rare
Kra 111 Dic odo:	14 " "	20 "	(7 " 1 ")	"
Kon 222 Dic odo:	22 " "	40 "	(6 " 1 ")	"
Hla 213 Dic elo:	32 " "	60 "	(6 " 1 ")	"
Maz 211 Hei/Dic:	46 " "	85 "	(6 " 1 ")	"
Nuw 111 Dic zub:	11 " "	21 "	(5 " 1 ")	"
Umk 111 Dic 2 spp:	197 " "	400 "	(5 " 1 ")	"
Lit 111 Dic/Hei:	51 " "	550 "	(1 " 1 ")	very rare

We include figures above only for those eight TCs yielding the greatest abundance of *Umkomasia*.

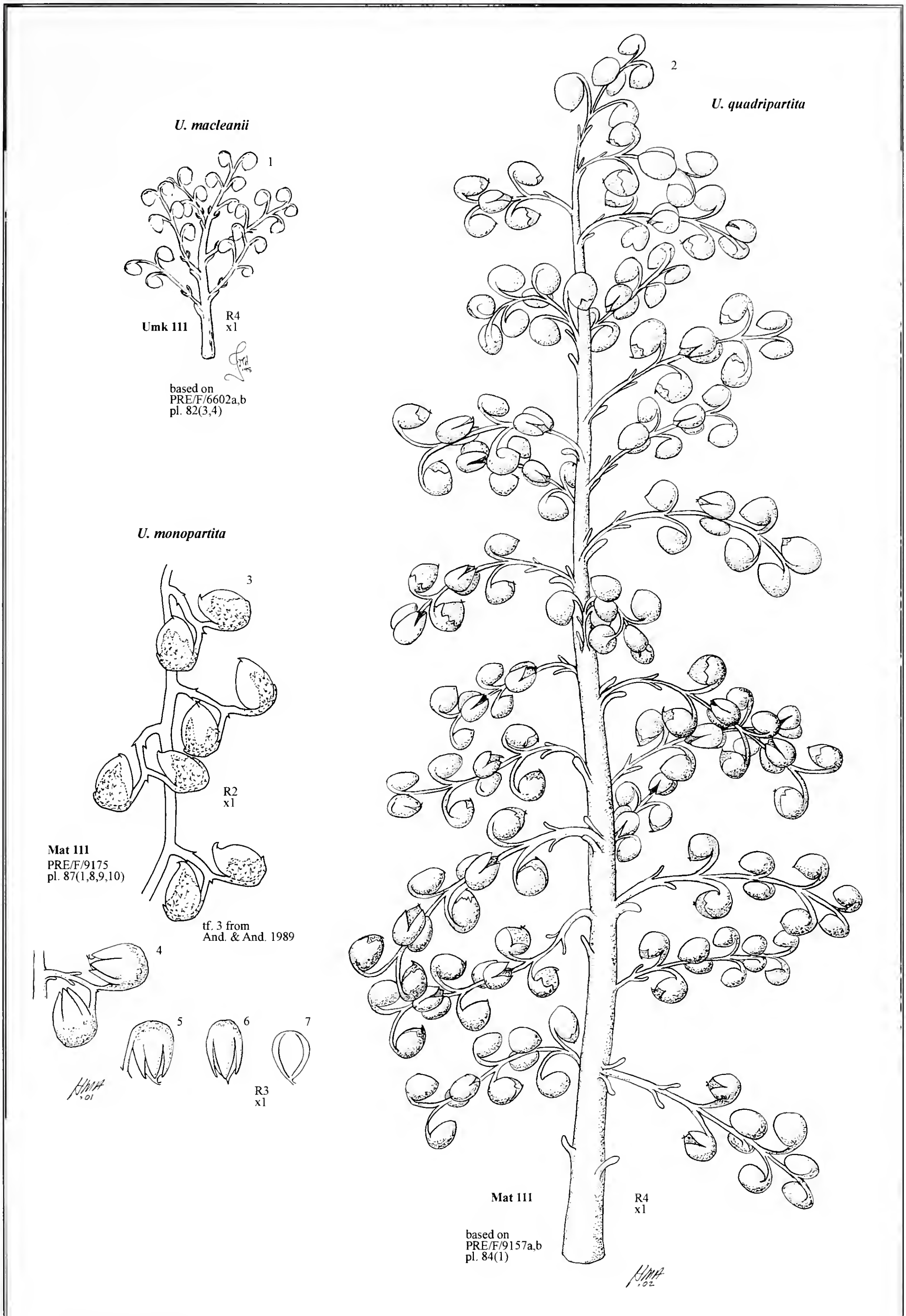
Affiliated organs
Male strobilus: *Pteruchus*—Grade 4 (Mut. occ., Cut. corr.).
Foliage: *Dicroidium*—Grade 4 (Mut. occ., Cut. corr.).

Classification & comparison
Suprageneric classification (Umkomasiaceae/Umkomasiales)
Umkomasia, along with its male (*Pteruchus*) and foliage (*Dicroidium*) affiliates—and the related ovulate strobilus *Fanerotheca*—are recognised here as the sole representatives of the family Umkomasiaceae and order Umkomasiales. *Peltaspermum* and the other five Gondwana Triassic ovulate genera included in the Ginkgoopsida (Tab. 30) are all considered too remote morphologically to be included in the same family or order.

Intergeneric comparison (Gondwana Triassic)
Fanerotheca, in its strobilus and cupulate megasporophylls, comes closest to *Umkomasia*. It differs mostly in the nature of its strongly winged seeds. *Kannaskoppia* resembles *Umkomasia* in its superficially similar cupulate units, but differs strongly in its forked architecture. Most other Molteno ginkgoopsid genera differ in not bearing cupulate structures.
Karibacarpon (not known from the Molteno) from the Upper Triassic Ripple-marked Flags, Lake Kariba, Zimbabwe, is a somewhat similar genus, but differs in its cupules splitting asymmetrically close to the pedicel attachment.

Cuticles
Potential sample: Lit 111, 51 indivs; Umk 111, 197 indivs.
Macerated: none in this work; see Thomas (1933).
Preservation grade: Grade 4–5.
Diagnostic characters: cells isodiametric to linear-oblong, end walls square to oblique, walls gently curved to sinuous, nonpapillate to papillate; trichome bases present; stoma orientation random; subsidiary cells brachyparacytic, nonlappetate; guard cells narrowly elliptic.
Comment: —
Significance:
Classification—The *Umkomasia* cuticle as described by Thomas (1933) and Townrow (1962) is comparable to that of *Dicroidium* as described by us (And. & And. 1983, 1989) and matches the general morphology characterising the class Ginkgoopsida. The main features in common are the narrowly elliptic guard cells and largely brachyparacytic and nonlappetate subsidiary cells.
Affiliations—The cuticle of *Umkomasia* supports affiliation with the leaf genus *Dicroidium* as first suggested by Thomas (1933). In the features described above (under 'Classification'), the *Umkomasia* cuticle is clearly more like that of *Dicroidium* than any of the other Molteno ginkgoopsid foliage genera, e.g. *Lepidopteris*, *Sphenobaiera*, *Ginkgoites* and *Dejerseya*. These latter taxa are all characterised by strongly lappetate, actinocytic subsidiary cells. The cuticles illustrated by Thomas are, in general, closest to those of *Dicroidium odontopteroides*.

Reconstructions
Strobilus
The well-preserved collection of intact strobili from the Molteno has added greatly to our knowledge of *Umkomasia*. The R4 reconstructions opposite are based on the almost complete strobili of *U. macleanii* from Umk111 (PRE/F/6602a,b), and of *U. quadripartita* from Mat 111 (BP/2/9157a,b). Minimal reconstruction was necessary and this mainly by straightening out the tip and adding the missing megasporophylls. No complete reconstructions for the other Molteno species are provided. Comparative R3 sketches (p. 244) have been made of the megasporophyll, cupule and seed for all eight Molteno species.
Megasporophyll
The position and number of bracteoles on the megasporophyll varies uncertainly with the species. The bracteoles, being small and delicate, may be poorly preserved and thus may have been overlooked or become detached. In *U. quadripartita* there appear two pairs on the megasporophyll peduncle (at base and midway), with single bracteoles also occurring isolated along the main axis as shown in the reconstruction.
Cupule
The partly decussate nature of the cupules shown in *U. quadripartita* is supported by the almost 3D preservation occurring at Aas 411, where *U. decussata* has sessile and undoubtedly decussate cupules.
Seeds/ovules
From *Umkomasia* ovules that are preserved as compressions it is difficult to determine whether, in life, they were bilaterally or radially symmetrical. At Aas 411, where they are preserved in an almost 3D state, the cupules are flattened even when viewed laterally (pl. 86). If they were radial then this view should also be circular. We interpret *Umkomasia* ovules/seeds in general as being bilaterally symmetrical and platyspermic in cross section.



U. macleanii
1
Umk 111
R4
x1
based on
PRE/F/6602a,b
pl. 82(3,4)
U. monopartita
3
R2
x1
Mat 111
PRE/F/9175
pl. 87(1,8,9,10)
tf. 3 from
And. & And. 1989
4
5
6
7
R3
x1
2
U. quadripartita
Mat 111
R4
x1
based on
PRE/F/9157a,b
pl. 84(1)

Tab. 51

UMKOMASIA HYPODIGM, Gondwana Triassic occurrence

AUTHOR		SUBREGION		FORMATION		LOCALITY	NAME	Indivs	ILLUSTRATION	Species: Molteno								Species: Other				Intactness		
										U. macleani	*U. stipulata*	*U. quadripartita*	*U. decussata*	*U. monopartita*	*U. gracilliaxis*	*U. cupulata*	*U. grandis*	*U. distans*	*U. sessilis*	*U. polycarpa*	*U. spp. indet*	Intact strobilus	Fragm. strobilus	Isolated heads
SOUTH AMERICA																								
1944a	Frenguelli	Barreal	NA2	22	Barreal	Punto 11	*Zuberia zuberi*	1	tf 10,11, pl 10(2–8)	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-
1980	Petriella	El Tranquilo	SA3	23	El Tranquilo	Estancia El Tranquilo	*Umkomasia macleani*	1	pl 2(4), f 1(f)	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-
"	"	Barreal	NA2	?	?	?	" *speciosa*	3	pl 2(5–7), f 1(c,d)	-	-	-	-	-	-	-	-	-	-	-	3	-	-	3
"	"	?	?	?	?	?	" sp.	1	pl 2(8), f 1(e)	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-
SOUTH AFRICA																								
1931	Thomas	Underberg	Ka4	24	Molteno Fm.	Umkomaas	*Umkomasia*	3	f 8(A–C)	3	-	-	-	-	-	-	-	-	-	-	-	1	1	1
1933	"	"	"	"	"	"	" *macleani*	1	f 1–4, pl 23(56)	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-
"	"	"	"	"	"	"	" *verrucosa*	1	f 5–8, pl 23(57)	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-
"	"	"	"	"	"	"	*Pilophorosperma granul.*	2	f 9–11, pl 23(58)	1	-	-	-	-	-	-	-	-	-	-	-	1	1	-
"	"	"	"	"	"	"	" *gracile*	1	f 12–13, pl 23(59)	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-
"	"	"	"	"	"	"	" *geminatum*	1	f 14	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-
"	"	"	"	"	"	"	" *paucipartitum*	1	f 15–16, pl 23(63)	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-
"	"	"	"	"	"	"	" *bumerense*	1	f 18,19, pl 23(60)	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-
"	"	"	"	"	"	"	" *crassum*	1	f 20,21,23(62)	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-
"	"	"	"	"	"	"	" *costulatum*	1	f 22–24	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-
"	"	"	"	"	"	"	" *natalense*	1	f 25,26	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-
"	"	"	"	"	"	"	" sp., Type A	1	f 27, pl 23(64), 24(65)	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-
"	"	"	"	"	"	"	" sp., Type B	1	f 28,29	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1
"	"	"	"	"	"	"	" sp., Type C	1	f 30(a)	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1
"	"	"	"	"	"	"	" spp.	1	f 30(b), pl 23(61)	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1
"	"	"	"	"	"	"	*Spermatacodon sewardi*	1	f 31,32, pl 24(66)	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-
1955	" (specimen repeated from Thomas 1993 f.1)						*Umkomasia macleani*	*	f 5(A)	*	-	-	-	-	-	-	-	-	-	-	-	*	-	-
1978–1999 Anderson & Anderson Molteno literature not considered in this table																								
ANTARCTICA																								
1996	Taylor	Allan Nunatak	TA1	22	Lashly Fm.	Allan Hills (Loc.?)	*Umkomasia* sp.	1	pl 4(2)	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
NEW ZEALAND																								
1956	Bell *et al.*	Benmore Dam	NZ4	21	Bl. Jacks Congl.	1km E of Benmore Dam	? *Corystospermaceae*	1	f 1(15)	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
1980a	Retallack	Mr. Potts	NZ3	"	Tank Gully CM	Tank Gully	*Pilophorosperma cf. cost.*	1	f 5(B), p 10(C)	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
"	"	"	"	"	"	"	" sp. A.	1	f 5(D)	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
1983	"	Benmore Dam	NZ4	21	Bl. Jacks Congl.	near Benmore Dam	" sp. indet.	2	f 6(B,C)	-	-	-	-	-	-	-	-	-	-	-	2	-	-	2
"	"	"	"	"	"	"	" sp. A.	2	f 6(D,E), pl 10(K,L)	-	-	-	-	-	-	-	-	-	-	-	2	-	-	2
1994	Pole & Rain	Invercargill	"	"	?	Pollack Rd.	? *Umkomasia* sp.	1	f 5(H), 6(A–B)	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-
AUSTRALIA																								
1888	Johnston	Hobart	Ta5	25	Brady equiv.	Lord's Hill (Hobart)	*Baiera tenuifolia*	1	pl 27(2B)	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-
1898	Shirley	Ipswich/Esk	CM5	24	Blackst. Stage	Denmark Hill	*Baenia geminata*	6	f 20(1,3,4)	-	-	-	-	-	-	-	-	-	-	-	6	1	1	4
1917b	Walkom (specimens repeated from Shirley 1898)						Gymnospermous seed	*	pl 8(6–9)	-	-	-	-	-	-	-	-	-	-	-	*	*	*	*
1947	Jones & de J.	Ipswich/Esk	CM5	23	Tivoli Stage	Por. 78, Chuwar (loc.21)	*Williamsonia* sp.2	1	tf 23	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
"	"	"		"	"	Woodend (loc.19)	Megasporophyll	1	tf 52	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-
1973⁺	Retallack	Sydney	Sy3	?	?	?	-	3	f 19(B), pl 17(1–3,5,6)	-	-	-	-	-	-	-	-	-	-	-	4	-	1	3
1974	Pledge	? Springfield	SA?	22	?	?	*Umkomasia*	2	pl 7(3,4)	-	-	-	-	-	-	-	-	-	-	-	2	-	1	1
1976	Mosel	Springfield B	SA2	22	(unnamed)	Central mesa	-	1	f 5(4), pl 16(1–4)	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-
"	White & Ye.	Mt. Ernest	Ca3	11	Culvida Sdst.	Minnie Range	*Baenia gracilis*	1	pl 13(49)	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-
1977a	Retall. *et al.*	Nymboida	CM7	19	Cloughers Cr.	UNEL 1564 (Kanga. Cr.)	*Pilophorosperma* cf. cost.	3	f 8(E–G)	-	-	-	-	-	-	-	-	-	-	-	3	1	-	2
1982	Holmes	Dubbo	Sy1	18	(unnamed)	Benolong (Ugothery)	? *Umkomasia* sp. A & B	2	pl 7(G,H)	-	-	-	-	-	-	-	-	-	-	-	2	-	2	-
"	Playf. *et al.*	Carnarvon	Bo5	19	Moolayember	Spring Creek	*Umkomasia geminata*	1	pl 5(1–2)	-	-	-	-	-	-	-	-	-	-	-	?1	1	-	-
"	" (specimens repeated from Shirley 1898)						" "	*	pl 5(7–9)	-	-	-	-	-	-	-	-	-	-	-	*	*	-	*
1986	White	Dubbo	Sy1	18	(unnamed)	Benolong (Ugothery)	*Umkomasia*	1	ph on p 148(221)	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-
"	"	Blue Mts.	Sy2	8	Banks Wall	Clarence Siding	*Dicroidium* 'flowers'	1	ph on p 149(222)	-	-	-	-	-	-	-	-	-	-	-	?1	-	1	-
"	"	"	"	"	"	Mt. Piddington	*Dicroidium* 'flowers'	1	ph on p 149(223)	-	-	-	-	-	-	-	-	-	-	-	?1	-	1	-
1987	Holmes	Ipswich/Esk	CM5	19	Esk Fm.	Ottaba (loc. 4110)	*Umkomasia polycarpa*	1	pl 2(A,B), f 1	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-
"	"	Nymboida	CM7	19	Basin Creek	Nymboida Q (UNEL 1489)	" *distans*	3	pl 4(A–D), f 3	-	-	-	-	-	-	-	-	3	-	-	-	3	-	-
"	"	"	"	"	"	" "	" *sessilis*	2	pl 6(A–C), f 5	-	-	-	-	-	-	-	-	-	2	-	-	2	-	-

⁺ unpublished

* specimens repeated—number of individuals therefore not given

Exclusions & synonyms

Gondwana Triassic

A new *Umkomasia* species, *U. unirama*, was described from the Shackleton Glacier region, Antarctica, from either the Upper Fremouw or Lower Falla Fm. by Axsmith *et al.* (2000). This unique strobilus has an axis bearing a whorl of four to eight cupules at the end of elongate stalks (peduncles). The whorled structure differentiates it from any other known *Umkomasia* species. It is somewhat similar to the genus *Matatiella* (p. 172) which has an ovule/seed-bearing palmate structure but no clear cupules. The Antarctic species, with the single axis bearing cupules in a subapical whorl would considerably expand the generic diagnosis of *Umkomasia*. We consider that its placement in *Umkomasia* is doubtful and that it should probably be placed in a new genus and possibly a new family and order in the Ginkgoopsida. We have not included it in our hypodigm for *Umkomasia*.

The fertile specimens referred to *U. unirama* are attached to short shoots on a branch similar to the mature long shoot in extant *Ginkgo biloba*. Another specimen from the same outcrop bears a single *Dicroidium* leaf apparently attached directly to a mature long shoot which also has short shoots similar to those on the fertile specimen. This would be the first record of *Umkomasia* attached to a short shoot, and of a *Dicroidium* leaf attached singly and laterally to a long shoot and not fascicled and terminal as suggested by our Molteno material. As the ovulate structure and leaf are not actually attached to the same branch or the leaf to a short shoot, the 'unequivocal evidence' (Axsmith *et al.* 2000) for Grade 5 affiliation is missing.

Structurally preserved ovules have been described from the Upper Fremouw Fm. of Antarctica as *Ignotospermum monilii* (Perovich & Taylor 1989). These are radially symmetrical and similar in shape and size (3.0 ∞ 3.75 mm) to seeds/ovules of *Umkomasia macleanii* but unlike any of the other Molteno ovulate genera. They have not been found with the typical bifid micropyle or with the associated cupules as in *Umkomasia*.

Holmes (1987) synonymised the genera *Pilophorosperma* and *Karibacarpon* with *Umkomasia* and mentioned that *Spermatocodon* (based on one poor specimen by Thomas 1933) was problematical. We consider *Spermatocodon* to be a poorly developed fragment of an unidentifiable *Umkomasia* species and it is here synonymised with *Umkomasia*.

The ovulate genus *Karibacarpon*, described together with its seed *Sengwacarpon* by Lacey (1976) from the Upper Triassic Ripple-marked Flags, Lake Kariba, Zimbabwe, and by Holmes & Ash (1979) from the Camden Head Claystone of the Lorne Basin, eastern Australia, is here regarded as distinct from *Umkomasia*. It differs in the cupule splitting asymmetrically close to the pedicel attachment. However, at both the Zimbabwean and Australian localities, *Karibacarpon* is closely associated with *Dicroidium* leaves.

Comparisons beyond Gondwana Triassic

Laurasian Triassic

Umkomasia franconia was described by Kirchner & Müller (1992) from the Rhaeto-Liassic of the Bayreuth area (Grossbellhofen and Unternschreez), Germany. We believe this fructification should be placed in a genus separate from *Umkomasia*. The German material was associated with the leaf genus *Thinnfeldia* and is clearly linked to that genus by the similar cuticle structure.

Other ages

An *Umkomasia* sp. has been recorded by Lejal-Nicol (1975) from the Jurassic of Libya. Fragmentary pinnae from the same locality were described as *Dicroidium*, *Pachypteris* and *Thinnfeldia*. There are no generic characters available to confirm the presence of *Dicroidium* leaves and we doubt the assignment of the ovulate structure to *Umkomasia*.

Gondwana Triassic occurrence (elaborated)

Umkomasia, after *Fanerotheca*, is the second most frequent (22 TCs, Tab. 52) and the most abundant (503 indivs) female strobilus in the Molteno (Tabs 6b, 9a, 11). It is the most widely recorded through the Gondwana Triassic. The largest collections are from South Africa (Tab. 52), followed by eastern Australia (Tab. 51).

The first described records of the female fruit of *Dicroidium*, now placed in *Umkomasia*, are those of Johnston (1888) from Tasmania. Holmes (1987) described three species: *U. polycarpa* from the Esk Fm. of Queensland; *U. distans* and *U. sessilis* from the Middle Triassic Basin Creek Fm. of eastern Australia. However, all other specimens (see Tab. 51) are too inadequately preserved or recorded to identify to species level.

Adaptive radiation (Molteno diversity)

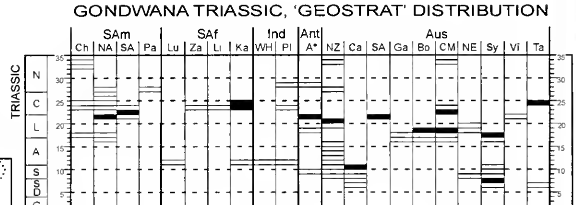
In his original monograph describing the genus *Umkomasia*, based on 'about 30 specimens of seed-bearing structures' from Umkomaas (Umk 111), Thomas (1933) recognised three genera (*Umkomasia*, *Pilophorosperma* and *Spermatocodon*) including 11 species. From our more extensive collection of 197 specimens from Umk 111, we believe that we have a better understanding of the natural range of variation within the once living populations. Based on the collections of both Thomas and ourselves, we recognise two palaeodemes and two species: *U. macleanii* is by far the most abundant; *U. monopartita* (also from Mat 111) is rare. The latter was not found or described by Thomas (1933).

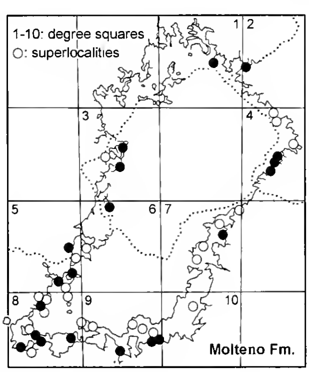
From our collections—*ca* 503 individuals from 22 TCs—we recognise eight species of *Umkomasia*. The diagnostic characters are based on the size and laxness or compactness of the strobilus and on the number and arrangement of cupules in the megasporophyll. This level of diversity is not reflected in the male affiliate *Pteruchus*, with only three species recognised.

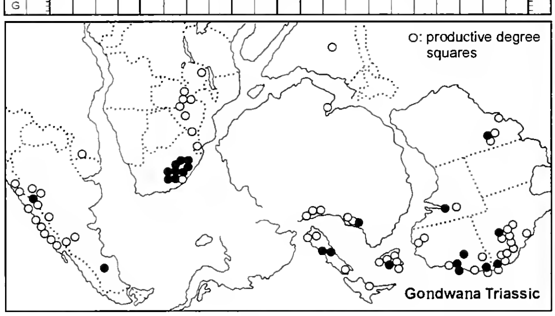
Most species derive from *Dicroidium* riparian forest and from Cycle 2 (Indwe Member). The eight species, based mostly on substantial palaeodemes from different TCs, are as follows:

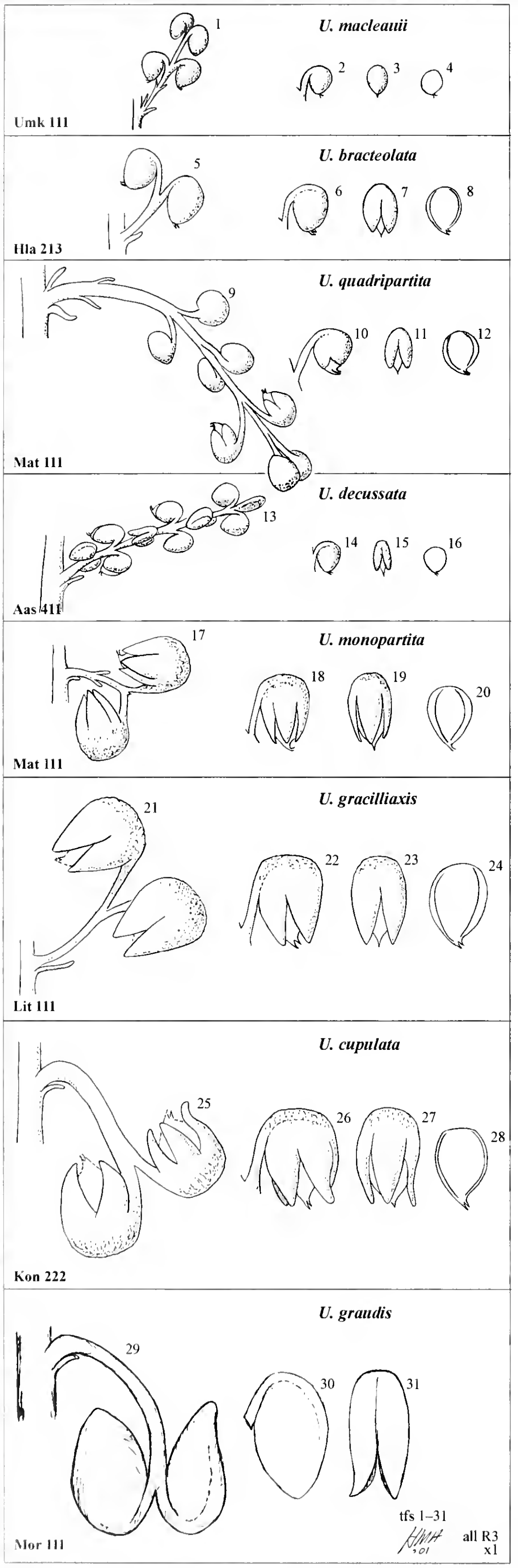
U. macleanii—Umk 111 Dic 2 spp (Umkomaas Valley), 175 indivs
Dicroidium riparian forest (mature); Cycle 2b (Indwe Member)
U. bracteolata—Hla 213 Dic elo (Hlatimbe Valley), 3 indivs
Dicroidium riparian forest (immature); Cycle 2b (Indwe Member)
U. quadripartita—Mat 111 Dic dub (Matatiele), 30 indivs
Dicroidium riparian forest (immature); Cycle 2b (Indwe Member)
U. decussata—Aas 411 Dic/Sph (Aasvoëlberg), 7 indivs
Sphenobaiera closed woodland; Cycle 1 (Bamboesberg Member)
U. monopartita—Mat 111 Dic dub (Matatiele), 45 indivs
Dicroidium riparian forest (immature); Cycle 2 (Indwe Member)
U. gracilliaxis—Lit 111 Dic/Hei (Little Switzerland), 42 indivs
Dicroidium riparian forest (mature); Cycle 2a (Indwe Member)
U. cupulata—Kon 222 Dic odo (Konings Kroon), 20 indivs
Dicroidium open woodland (floodplain); Cycle 2f (Mayaputi Member)
U. grandis—Mor 111 Dic odo (Morija), 3 indivs
Dicroidium open woodland (floodplain); Cycle 2c (Indwe Member)

GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION









Molteno *Umkomasia* species, a comparative study

***Umkomasia macleanii*—Umk 111**
Strobilus: small (*ca* 40 x 35 mm).
Megasporophyll: erect, bearing 2 or 3 pairs of pedicellate cupules; bracteoles usually in 2 pairs, at base and midway along peduncle.
Cupule: small, circular to ovate, unlobed.
Seed: circular, wing not evident.

***U. bracteolata*—Hla 213**
Strobilus: small to medium (*ca* 55 x 30 mm).
Megasporophyll: erect, bearing a single pair of pedicellate cupules; bracteole single, abaxial at base of peduncle.
Cupule: medium, circular to ovate, 2-lobed.
Seed: circular to ovate, wing narrow (incipient).

***U. quadripartita*—Mat 111**
Strobilus: medium to large (*ca* 150 x 80 mm).
Megasporophyll: reflexed, bearing 3 or 4 pairs of pedicellate, partly decussate cupules; bracteoles usually in 2 pairs, at base and midway along peduncle.
Cupule: small to medium, relatively circular to ovate, 2-lobed (mainly).
Seed: circular to ovate, wing narrow to medium.

***U. decussata*—Aas 411**
Strobilus: medium to large (to ?120 x 60 mm).
Megasporophyll: semi-erect, bearing up to 7 strongly decussate pairs of sessile cupules; bracteole single, abaxial at base of peduncle.
Cupule: small, roundly triangular, 2-lobed (mainly).
Seed: circular, wing not evident.

***U. monopartita*—Mat 111**
Strobilus: medium to large (>100 x 38 mm).
Megasporophyll: reflexed, bearing a single pair of pedicellate cupules; bracteoles variable, usually single at abaxial base and paired midway along peduncle.
Cupule: medium, roundly triangular, 4-lobed.
Seed: circular to ovate, wing medium.

***U. gracilliaxis*—Lit 111**
Strobilus: large (>100 x 50 mm), distinctly lax; axis gracile.
Megasporophyll: erect to reflexed, bearing a single pair of pedicellate cupules; bracteole single, elongated, abaxial at base of peduncle.
Cupule: medium to large, roundly triangular, 4-lobed.
Seed: ovate, wing narrow to medium.

***U. cupulata*—Kon 222**
Strobilus: large (>100 x 40 mm), axis of medium girth.
Megasporophyll: reflexed, bearing a single pair of pedicellate cupules; bracteole single, abaxial at base of peduncle.
Cupule: large, roundly triangular, 4- or 5-lobed.
Seed: ovate, wing narrow.

***U. grandis*—Mor 111**
Strobilus: large (far >110 x 64 mm), axis robust.
Megasporophyll: reflexed, bearing a single pair of sessile cupules; bracteole single, abaxial at base of peduncle.
Cupule: large, ovate, 2-lobed.
Seed: unknown.

assemblages (taphocoenosis)	Genera				Species									Intactness		
	Dicroidium	♀ *Umkomasia*	♂ *Pteruchus*	♀ *Fanerotheca*	*U. macleanii*	*U. bracteolata*	*U. quadripatrita*	*U. decussata*	*U. monopartita*	*U. gracilliaxis*	*U. cupulata*	*U. grandis*	*U. spp indet*	Intact strobilus	Partial strobilus	Isolated megasp.
Ken 111 Dic cra	**99**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nav 111 Dic odo	**98**	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Cal 111 Dic/Sph	**50**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bir 211 Sph 2spp	**4**	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Bir 311 Hei/Sph	**14**	2	1	2	-	-	-	-	-	-	-	-	2	1	1	-
Bir 111 " "	**1**	-	-	60	-	-	-	-	-	-	-	-	-	-	-	-
Gre 121 Hei elo	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 111 Equ sp	**2**	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
Boe 111 Lep sto	5	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
" " Dic/Hei	**57**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 112 Dic cor	**99**	8	10	-	8	-	-	-	-	-	-	-	-	1	1	6
Cyp 111 Dic cra	**75**	2	-	1	-	-	-	-	-	-	-	-	2	-	-	2
Mol 111 Sph pon	12	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Kan 112 Hei elo	**1**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tel 111 " "	**6**	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-
Kom 111 Sph/Dic	**39**	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
Vin 111 Dic odo	**70**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ela 111 " "	**87**	1	3	1	-	-	-	-	-	-	-	-	1	-	1	-
Kra 311 " "	**99**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 221 Beetles	**50**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 111 Dic odo	**90**	14	30	-	-	-	13	-	1	-	-	-	-	1	3	10
Lut 111 Hei/Dic	**40**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 411 " "	**50**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 311 Hei elo	58	-	-	7	-	-	-	-	-	-	-	-	-	-	-	-
" 221 Equ sp	**1**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tin 121 Sph 2spp	**1**	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Wal 111 Dic odo	**92**	-	-	24	-	-	-	-	-	-	-	-	-	-	-	-
Kon 223 " "	**80**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 222 " "	**87**	22	13	1	-	-	-	-	-	-	20	-	2	-	5	17
" 211 Hei elo	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 111 Dic odo	**78**	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
" " Hei elo	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pen 321 Dic/Ris	**51**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 211 Dic/Equ	**50**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 221 " "	**40**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 511 Equ sp	**2**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 421 Dic odo	**89**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 431 Dic/Equ	**40**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 311 Hei elo	**25**	3	4	-	-	-	-	-	-	-	-	-	3	-	1	2
" 411 " "	13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kle 111 Hei/Dic	**45**	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Kap 111 Dic/Ris	**50**	2	11	40	-	-	-	-	-	-	-	-	2	1	-	1
Ela 112 Equ sp	**1**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" " Dic/Hei	**60**	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
Nuw 111 Dic zub	**70**	11	15	-	-	-	11	-	-	-	-	-	-	1	4	6
" 211 Dic 2spp	**98**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Win 111 Hei elo	**10**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mor 111 Dic zub	**99**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" " Dic odo	**98**	3	1	-	-	-	-	-	-	-	-	3	-	-	1	2
Qua 111 " "	**40**	1	-	-	1	-	-	-	-	-	-	-	-	-	-	1
Mak 111 " "	**90**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Maz 111 Dic cra	**74**	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-
" 211 Hei/Dic	**64**	46	27	5	29	-	-	-	-	17	-	-	-	3	3	40
Moo 111 Dic zub	**99**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hla 111 Equ sp	**1**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 211 Dic 3spp	**85**	3	2	3	-	-	-	-	3	-	-	-	-	-	-	3
" 212 " "	**91**	4	4	-	-	-	-	-	4	-	-	-	-	-	-	4
" 213 Dic elo	**89**	32	20	5	28	3	-	-	-	1	-	-	-	5	7	20
Umk 111 Dic 2spp	**69**	197	138	16	175	-	-	-	22	-	-	-	-	25	55	117
Cha 111 Dic odo	**100**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 211 Dic dub	**80**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Inj 111 Dic odo	**100**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 211 Dic dub	**90**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
San 111 Dic cra	**90**	4	5	5	2	-	-	-	-	2	-	-	-	-	1	3
Mng 111 Dic 2spp	**93**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Qac 111 Hei/Dic	**50**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mat 111 Dic dub	**89**	75	84	6	-	-	30	-	45	-	-	-	-	8	33	34
Gol 111 " "	**99**	1	1	-	-	-	-	-	-	-	-	-	1	-	1	-
Lit 111 Dic/Hei	**50**	51	36	3	9	-	-	-	-	42	-	-	-	1	10	40
Aas 111 Hei elo	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 311 " "	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
" 411 Dic/Sph	**60**	7	3	47	-	-	-	7	-	-	-	-	-	1	3	3
" 511 Dic elo	**50**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ask 111 Equ sp	**21**	14	15	-	14	-	-	-	-	-	-	-	-	-	1	13
Bam 111 Dic dub	**98**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total TCs	75	22	22	27	8	1	3	1	5	4	1	1	7	10	17	18
Total indivs	%	503	425	247	266	3	54	7	75	62	20	3	13	48	131	324

Tab. 52. ***Umkomasia*****, Molteno occurrence**

Evidence for affiliation of organs

Literature

Since Thomas (1933) described and affiliated *Umkomasia* and *Pteruchus* with *Dicroidium*, this affiliation has been widely accepted (Crane 1988; Retallack & Dilcher 1988) and is fully supported by our research (And. & And. 1983, 1989).

In the last decade, excellently preserved permineralised fossils have been described from one locality in the Fremouw Formation in the Beardmore Glacier region of Antarctica by the Taylors and their colleagues. This material links *Dicroidium* leaves and stems with *Pteruchus* and *Umkomasia* on the basis of vascular structure (Perovich & Taylor 1989; Pigg 1990; Meyer-Berthaud *et al.* 1993; Osborn & Taylor 1993; Yao *et al.* 1995). A recent paper on Antarctic material (Axsmith *et al.* 2000) is discussed under 'Exclusions & synonyms' above.

Mutual occurrence

In the Molteno, *Umkomasia* occurs at 22 TCs (Tab. 52) where, in most cases, *Dicroidium* is a dominant element of the flora. The remaining 53 TCs (Tab. 52) that have not yet yielded *Umkomasia* are mostly under-collected (Tab. 1, man-hours collecting). *Umkomasia* and *Pteruchus* have both been collected at 22 TCs. (A discussion on this co-occurrence is provided under *Pteruchus*, p. 253.) At two TCs (Cyp 111, Qua 111), *Umkomasia* is present but *Pteruchus* has not been found. There is also the puzzling affiliation of *Fanerotheca* (p. 274) and its apparent association with *Dicroidium* at Bir 111 and Wal 111.

Cuticular correspondence

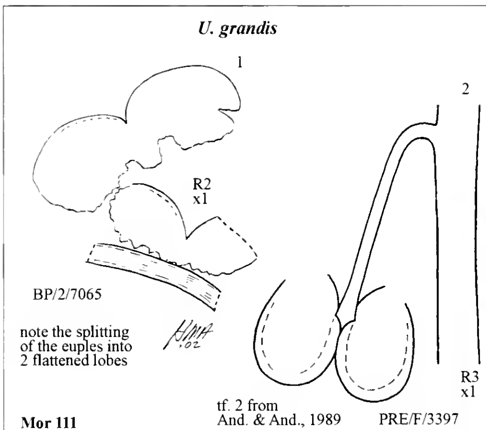
This was first noted by Thomas (1933) and more recently by Townrow (1962) for *Umkomasia*, *Pteruchus* and *Dicroidium*. Further details are given under 'Cuticles' (p. 240).

Species level affiliations

The question of which *Umkomasia* species affiliates with which *Dicroidium* species is addressed only peripherally here, and needs further resolution. We have made a preliminary correlation between the *Umkomasia* species occurring at the 22 TCs (Tab. 52) and the associated *Dicroidium* species (unpublished foliage-species/TC matrix table; see also And. & And. 1983, Tabs 6, 7; Figs 3–5, including 'pictograph series'). At some six TCs there is one dominant *Dicroidium* species (palaeodeme) and only one *Umkomasia* species, but no consistent pairing between the respective species emerges.

U. macleanii, occurring in eight TCs (and readily the most frequent ovulate species), reveals no clear tie with a particular *Dicroidium* species. It is most abundant at Umk 111 Dic 2spp (175 indivs) and could be linked to the *Dicroidium* palaeodeme encompassing *D. orbiculoides* 25% and *D. crassinervis* 13% (referred to as *D. odontopteroides* subsp. *orbiculoides* and *D. crassinervis* forma *obtusifolium* and forma *crassinervis* respectively in And. & And. 1983; see also Tabs 16, 17, this volume).

In spite of holding by far the largest (extensive-intensive) collection of *Umkomasia* and *Dicroidium* from any formation globally, we still do not have sufficient material to discern the patterns of affiliation at a species level.



Umkomasia macleanii H.H.Thomas 1933

Holotype
Specimen: V. 23360 (U11) in Nat. Hist. Mus., London.
Thomas (1933), fig. 1, pl. 23(56); refigured here, pl. 82(8).
Assemblage: Umk 111 Dic 2spp, Umkomaas Valley.
Preservation: a virtually complete strobilus; compression in thinly laminated, carbonaceous (good cuticle), moderately baked, dark grey shale with good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 175 indivs (25 intact, 50 partial, 100 isolated), pl. 82(1–7, 10–16). (This does not include the Thomas (1933) collection of some 30 specimens in the Nat. Hist. Mus., London.)

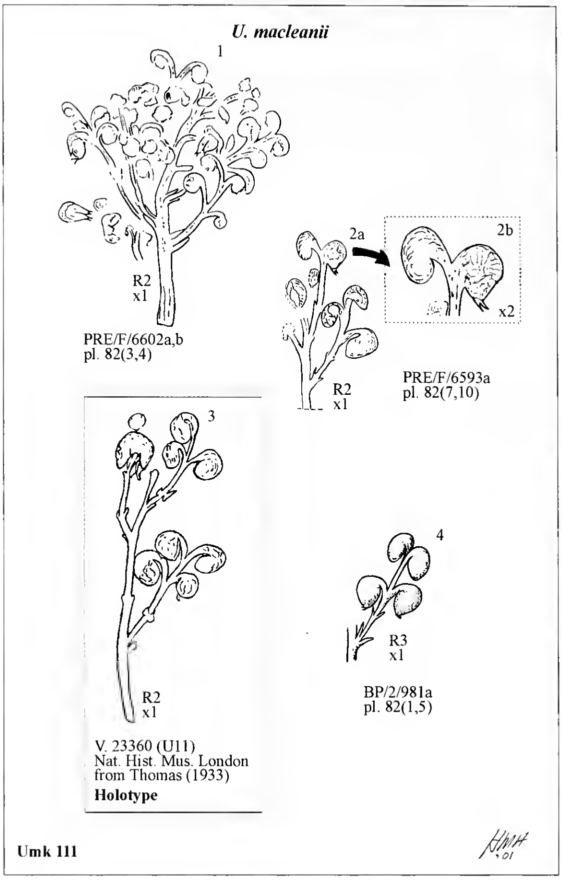
Sister palaeodemes—7 (best 3 listed)
Maz 211 Hei/Dic: 29 indivs (1 intact, 3 partial, 28 isolated), pl. 86(8–15).
Hla 213 Dic elo: 28 indivs (3 intact, 7 partial, 18 isolated).
Lit 111 Dic/Hei: 9 indivs (all isolated).

Specific diagnosis
An *Umkomasia* species with small compact strobili, bearing erect megasporophylls with 2 or 3 pairs of pedicellate cupules.

Specific characters
Strobilus: small (*ca* 40 x 35 mm).
Megasporophyll: erect, bearing 2 or 3 pairs of pedicellate cupules; bracteoles usually in 2 pairs, at base and midway along peduncle.
Cupule: small, circular to ovate, unlobed.
Seed: circular, wing not evident.

Eponymy
macleanii—in honour of Tom Maclean, farmer in the area at the time of Thomas's trip to South Africa.

Comment & comparison
U. macleanii is the most frequently occurring (eight TCs) and abundant of the eight Molteno *Umkomasia* species recognised here. The Umk 111 reference palaeodeme, with 175 individuals (including 25 more or less intact strobili), is by far the most fully represented *Umkomasia* palaeodeme from the formation. While Thomas (1933) recognised three genera with 14 species in his collection from the Umk 111 site, our interpretation of the material is that it all falls within this single species. The 22 remaining individuals in our collection from Umk 111 are identified as *U. monopartita* (Tab. 51) and have far larger fleshy appearing cupules and constitute a quite distinct palaeodeme.



Umkomasia bracteolata J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/8903a,b; pl. 83(1–4).
Assemblage: Hla 213 Dic 3spp, Hlatimbe Valley.
Preservation: virtually complete strobilus, with counterpart; compression in thinly laminated, carbonaceous (poor cuticle), medium dark grey shale with good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 3 indivs (1 intact, 2 partial), pl. 83(1–8).

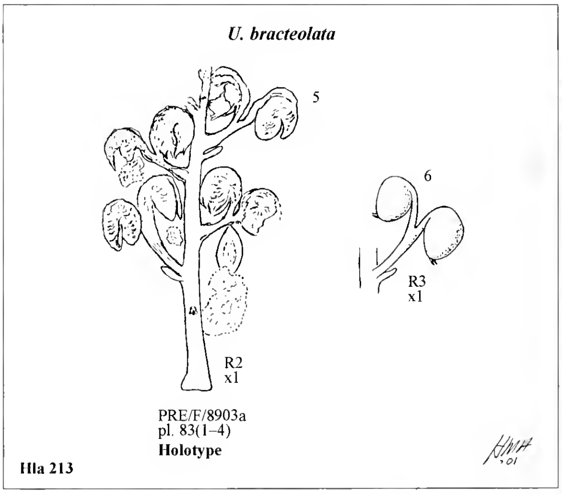
Sister palaeodemes—nil.

Specific diagnosis
An *Umkomasia* species with small to medium compact strobili, bearing erect megasporophylls with a single pair of pedicellate cupules.

Specific characters
Strobilus: small to medium (*ca* 55 x 30 mm).
Megasporophyll: erect, bearing a single pair of pedicellate cupules; bracteole single, abaxial at base of peduncle.
Cupule: medium, circular to ovate, 2-lobed.
Seed: circular to ovate, wing narrow (incipient).

Etymology
bracteolata—with reference to the bracteoles that are particularly well preserved.

Comment & comparison
This species, represented only by the very limited reference palaeodeme of three individuals (including one intact strobilus), is the least securely established of the eight Molteno *Umkomasia* species. It is distinguished from *U. monopartita* principally by size and the two-lobed rather than four-lobed cupules.



Umkomasia quadripartita J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/9157a,b; pls 84(1, 5), 85(1).
Assemblage: Mat 111 Dic dub, Matatiele.
Preservation: a virtually complete strobilus, part and counterpart; impression in thickly laminated, olive-grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 30 indivs (2 intact, 16 partial, 12 isolated), pls 84(1–5), 85(1–6); seeds, pl. 85(7–12), possibly (13–16).

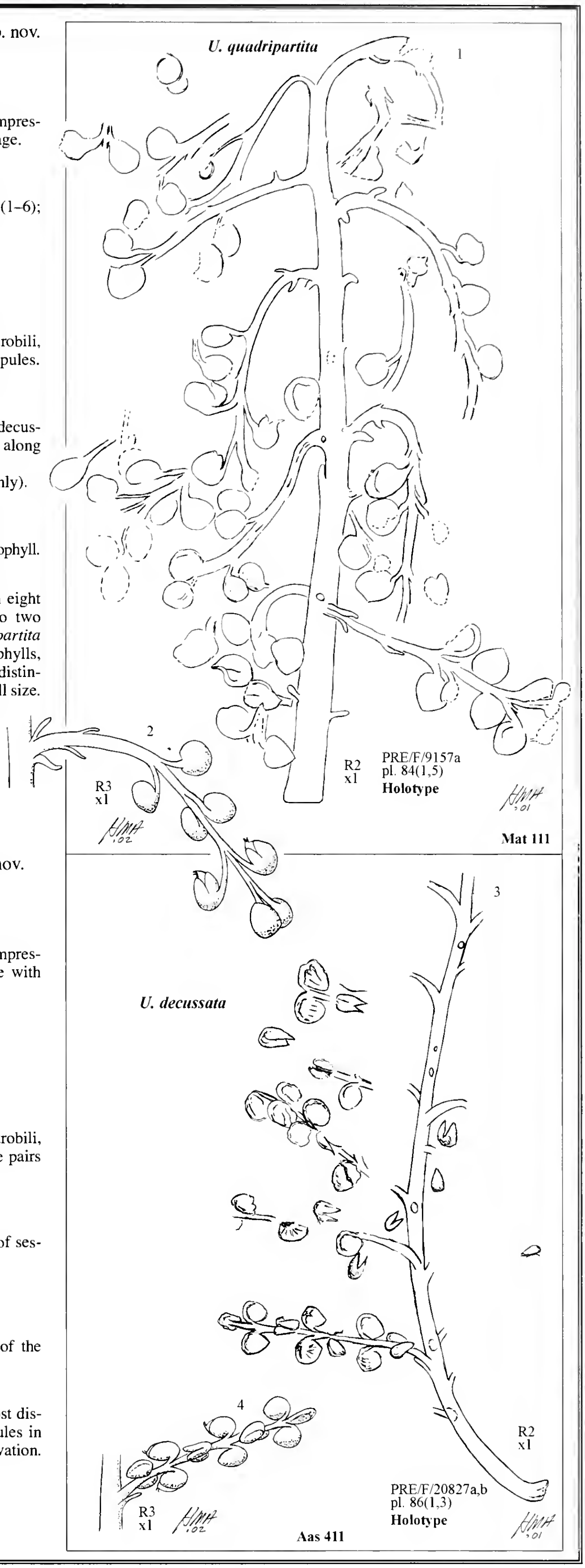
Sister palaeodemes—2 only (both listed)
Kra 111 Dic odo: 13 indivs (1 intact, 3 partial, 9 isolated).
Nuw 111 Dic zub: 11 indivs (1 intact, 4 partial, 6 isolated).

Specific diagnosis
An *Umkomasia* species with medium to large, relatively lax strobili, bearing reflexed megasporophylls with 3 or 4 pairs of pedicellate cupules.

Specific characters
Strobilus: medium to large (*ca* 150 x 80 mm).
Megasporophyll: reflexed, bearing 3 or 4 pairs of pedicellate, partly decussate cupules; bracteoles usually in 2 pairs, at base and midway along peduncle.
Cupule: small to medium, relatively circular to ovate, 2-lobed (mainly).
Seed: circular to ovate, wing narrow to medium.

Etymology
quadripartita—with reference to the four pairs of cupules per megasporophyll.

Comment & comparison
At Mat 111, the collection of 75 *Umkomasia* individuals (with eight intact and 33 partial strobili) can be fairly readily separated into two palaeodemes. These have been selected as reference for *U. quadripartita* and *U. monopartita* respectively. With its multi-ovulate megasporophylls, *U. quadripartita* compares most closely with *U. macleanii* but is distinguished in the greater number of cupule pairs and the far larger overall size.



Umkomasia decussata J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/20827a,b; pl. 86(1, 3).
Assemblage: Aas 411 Dic/Sph, Aasvoëlberg.
Preservation: a virtually complete strobilus, part and counterpart; impression in thinly laminated, strongly baked, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 7 indivs (1 intact, 3 partial, 3 isolated), pl. 86(1–7).

Sister palaeodemes—nil.

Specific diagnosis
An *Umkomasia* species with medium to large, relatively lax strobili, bearing semi-erect megasporophylls with up to 7 strongly decussate pairs of sessile cupules.

Specific characters
Strobilus: medium to large (up to ?120 x 60 mm).
Megasporophyll: semi-erect, bearing to 7 strongly decussate pairs of sessile cupules; bracteole single, abaxial at base of peduncle.
Cupule: small, roundly triangular, 2-lobed (mainly).
Seed: circular, wing not evident.

Etymology
decussata—with reference to the opposite-decussate arrangement of the cupules.

Comment & comparison
This extremely rare taxon, known only from Aas 411, is the most distinctive of the Molteno *Umkomasia* species in bearing sessile cupules in strongly decussate pairs. This is seen clearly in the almost 3D preservation.

Umkomasia monopartita J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/9175; pl. 87(1, 8, 9, 10).
Assemblage: Mat 111 Dic dub, Matatiele.
Preservation: incomplete strobilus, without counterpart; impression in thickly laminated, olive-grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 45 indivs (6 intact, 17 partial, 22 isolated), pl. 87(1–13).

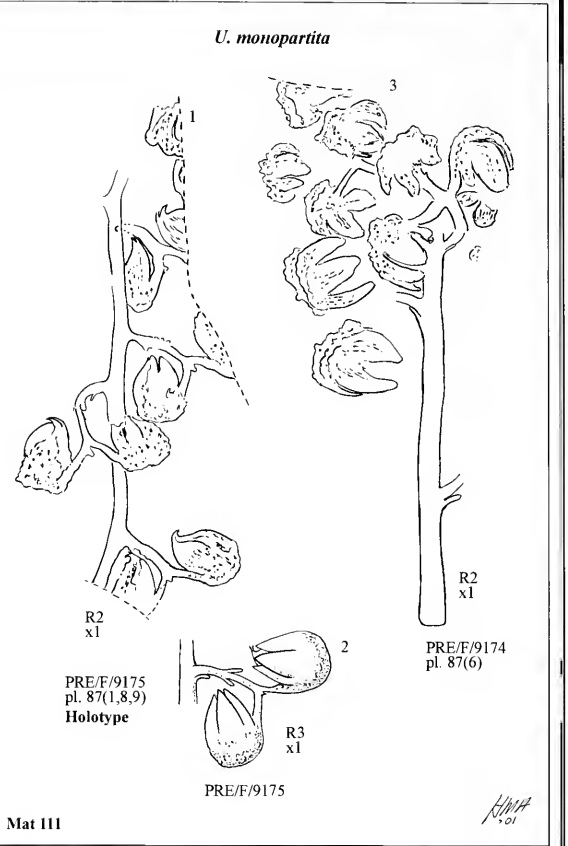
Sister palaeodemes—4 (best 1 listed)
Umk 111 Dic 2spp: 22 indivs (5 partial, 17 isolated).

Specific diagnosis
An *Umkomasia* species with medium to large, relatively lax strobili, bearing reflexed megasporophylls with a single pair of pedicellate cupules.

Specific characters
Strobilus: medium to large (>100 x 38 mm).
Megasporophyll: reflexed, bearing a single pair of pedicellate cupules; bracteoles variable, usually single at abaxial base and paired midway along peduncle.
Cupule: medium, roundly triangular, 4-lobed.
Seed: circular to ovate, wing medium.

Etymology
monopartita—with reference to the single pair of cupules per megasporophyll.

Comment & comparison
This well represented species shares a number of features with *U. gracilliaxis* and differs mainly in its more compact strobilus with shorter pedicels.



Umkomasia gracilliaxis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: BP/2/2110; pl. 88(1, 3).
Assemblage: Lit 111 Dic/Hei, Little Switzerland.
Preservation: incomplete strobilus, without counterpart; compression in thinly laminated, carbonaceous (good cuticle), dark grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 42 indivs (1 intact, 10 partial, 31 isolated), pl. 88(1–13).

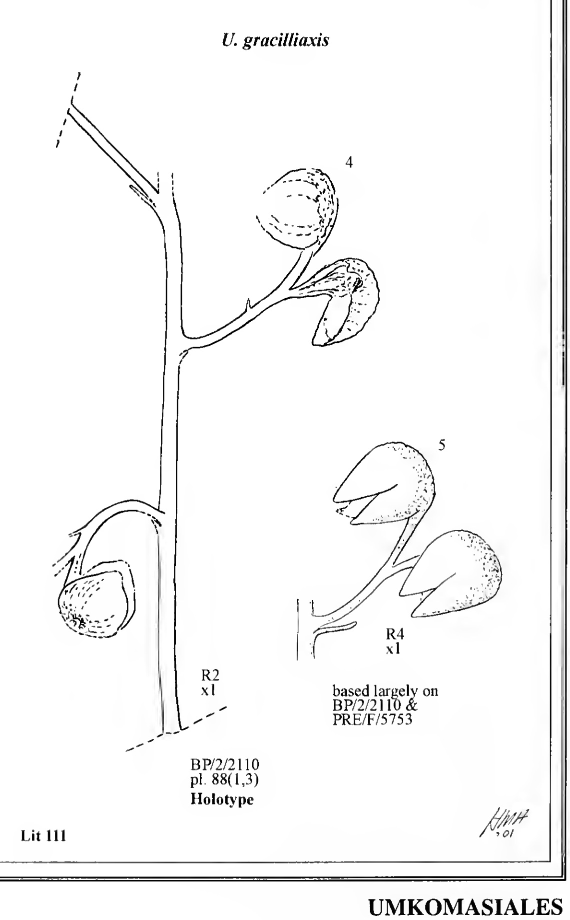
Sister palaeodemes—3 (best 1 listed)
Maz 211 Hei/Dic: 17 indivs (2 intact, 6 partial, 9 isolated).

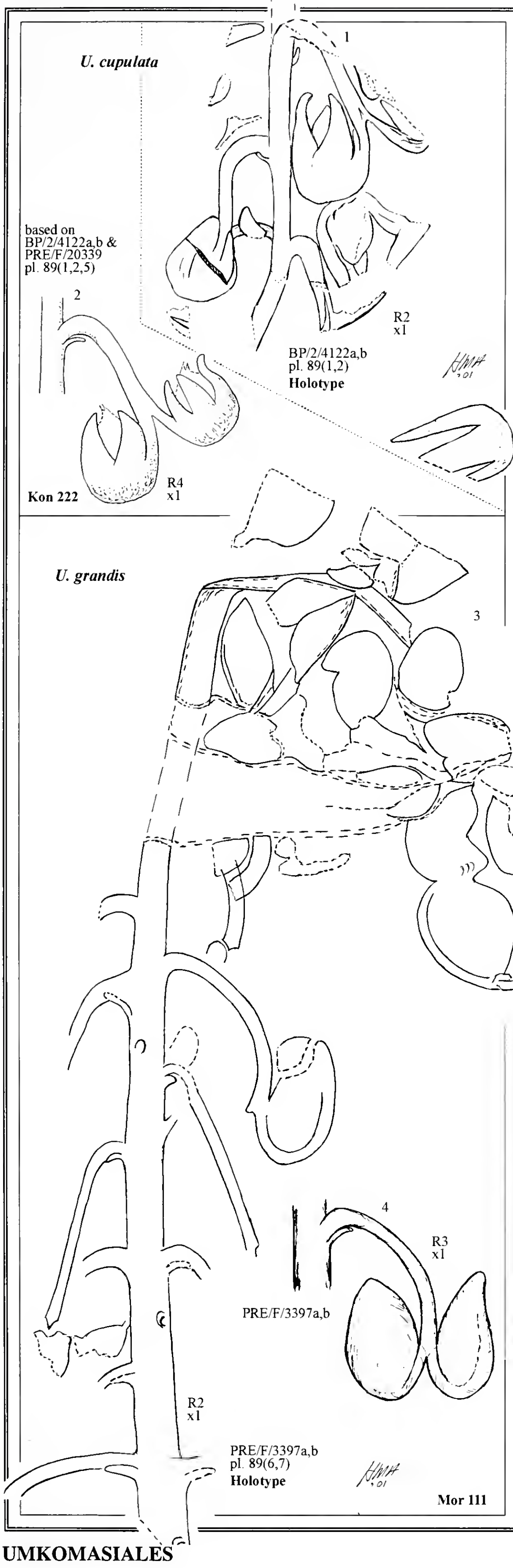
Specific diagnosis
An *Umkomasia* species with large lax strobili, bearing erect to reflexed megasporophylls with a single pair of pedicellate cupules.

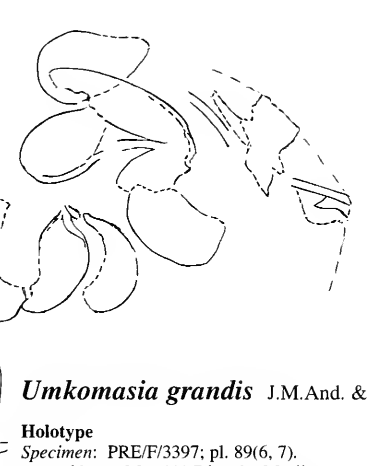
Specific characters
Strobilus: large (>100 x 50 mm), distinctly lax; axis gracile.
Megasporophyll: erect to reflexed, bearing a single pair of pedicellate cupules; bracteole single, elongated, abaxial at base of peduncle.
Cupule: medium to large, roundly triangular, 4-lobed.
Seed: ovate, wing narrow to medium.

Etymology
gracilliaxis—with reference to the gracile axis of the strobilus.

Comment & comparison
U. gracilliaxis has a particularly gracile and lax strobilus and it is mainly in this feature that it differs from all other Molteno *Umkomasia* species. It is closest in overall morphology to *U. monopartita* and *U. cupulata*.







Umkomasia cupulata J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: BP/2/4122a.b; pl. 89(1, 2).
Assemblage: Kon 222 Dic odo, Konings Kroon.
Preservation: fragmentary strobilus, part and counterpart, 3D mould and cast in thinly laminated, medium grey cherty shale with poor cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 20 indivs (5 partial, 15 isolated), pl. 89(1–5).

Sister palaeodemes—nil.

Specific diagnosis
An *Umkomasia* species with large relatively lax strobili, bearing reflexed megasporophylls with a single pair of pedicellate cupules.

Specific characters
Strobilus: large (>100 x 40 mm), axis of medium girth.
Megasporophyll: reflexed, bearing a single pair of pedicellate cupules; bracteole single, abaxial at base of peduncle.
Cupule: large, roundly triangular, 4- or 5-lobed.
Seed: ovate, wing narrow.

Etymology
cupulata—in recognition of the clear preservation of the cupules.

Comment & comparison
U. cupulata, known only from Kon 222, comes closest to *U. grandis* in size but the cupules are pedicellate (not sessile), roundly triangular (not oval) and split into four or five lobes (not two).

Umkomasia grandis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/3397; pl. 89(6, 7).
Assemblage: Mor 111 Dic odo, Morija.
Preservation: intact strobilus, no counterpart, impression in thickly laminated, light olive-grey shale with poor cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 3 indivs (1 intact, 2 isolated), pl. 89(6–8), p. 245, tf. 1.

Sister palaeodemes—nil.

Specific diagnosis
An *Umkomasia* species with large, robust, relatively lax strobili, bearing reflexed megasporophylls with a single pair of sessile cupules.

Specific characters
Strobilus: large (far >110 x 64 mm), axis robust.
Megasporophyll: reflexed, bearing a single pair of sessile cupules; bracteole single, abaxial at base of peduncle.
Cupule: large, ovate, 2-lobed.
Seed: unknown.

Etymology
grandis—with reference to the large size of the strobilus.

Comment & comparison
U. grandis, in life, would have been by far the largest of the Molteno *Umkomasia* species. It may easily have reached an impressive 0.3 m in length. The species differs from *U. cupulata* in its far greater overall size and in the megasporophylls bearing single pairs of sessile cupules which split into two lobes (not four or five).

Pteruchus H.H.Thomas 1933

Type species
Pteruchus africanus H.H.Thomas 1933.
Umkomaas Valley, Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis emended

A ginkgoopsid male strobilus of lax paniculate form, with simple to once-forked microsporophylls bearing terminal laminate heads with numerous abaxial microsporangia.

Generic characters

Strobilus: simple, lax, paniculate, radially symmetrical, small to large (30–200 mm long); axis robust, markedly tapering, erect to arching; microsporophylls fairly numerous, arrangement irregularly helical.

Microsporophyll: simple to once forked near base, planar; peduncle gracile; fertile heads single or paired, pedicellate, oval to linear oblong (5–40 mm long); laminae bilaterally symmetrical, margins undulate to strongly lobed; microsporangia numerous, pendent, densely packed to cover full abaxial surface of lamina.

Microsporangium: linear-elliptic (2–4 mm); ornamentation fine, linear, forking and converging.

Pollen: disaccate.

Etymology

Pteruchus—*pterona* (Gr), wing; Thomas (1933) described the microsporophyll as 'a wing-like thing'.

Global range: several spp., Gondwana, Tr. (SCY–CRN).
First: *Pteruchus feistmanteli* (*Pterorrachis barreal*) Retallack (1973).
Mt. Piddington, Banks Wall Fm., Blue Mts, Australia.
Last: *Pteruchus africanus* (*Baiera tenuifolia*) Johnston (1888).
Lord's Hill, Brady Fm., Hobart, Tasmania.

Gondwana Triassic occurrence (see *Pteruchus* hypodigm, Tab. 53)
SAm—N. Argentina & Patagonia, 5 TCs (12 indivs).
SAf—Karoo Basin, 22 TCs (431 indivs).
Ind—S. Rewa/Tiki, 1 TC (1 indiv.).
Ant—E. & Trans-Antarctica, 3 TCs (11 indivs).
Aus—Australia widespread, 13 TCs (33 indivs).
New Zealand, 2 TCs (2 indivs).

Molteno occurrence (see Tab. 54)
Frequency (F): 22 TCs (of 100 sampled in the Molteno).
Diversity (D): 3 species.
Abundance (A): 431 indivs total; rare to very rare in top 8 TCs.

Kra 111 Dic odo:	30	indivs in	20	man-hrs	cleaving	(15	per 1	man-day)	rare
Mat 111 Dic zub:	84	" "	65	"	"	(14	" 1	")	"
Nuw 111 Dic zub:	15	" "	21	"	"	(7	" 1	")	"
Kon 222 Dic odo:	13	" "	40	"	"	(3	" 1	")	"
Hla 213 Dic elo:	20	" "	60	"	"	(3	" 1	")	"
Maz 211 Hei/Dic:	27	" "	85	"	"	(3	" 1	")	"
Umk 111 Dic 2spp:	138	" "	400	"	"	(3	" 1	")	"
Lit 111 Dic/Hei:	36	" "	550	"	"	(1	" 2	")	v. rare

As for *Umkomasia*, we include above only those eight TCs yielding the greatest number of *Pteruchus* specimens. The pattern of occurrence of the reproductive affiliates of *Dicroidium* appears remarkably similar.

Affiliated organs
Female strobilus: *Umkomasia*—Grade 4 (Mut. occ., Cut. corr.).
Foliage: *Dicroidium*—Grade 4 (Mut. occ., Cut. corr.).

Classification & comparison

Suprageneric classification (Umkomasiaceae/Umkomasiales)

A group of six Gondwana Triassic male genera are included here in the Ginkgoopsida: *Antevsia* (Peltaspermales), *Switzianthus* (Matatiales), *Eosteria* (Ginkgoales), *Stachyopitys* (Hamshawviales), *Pteruchus* (Umkomasiales) and *Kannaskoppianthus* (Petriellales). Based on their female affiliates, which all differ significantly in morphological organisation, each is placed in a separate family and order.

Intergeneric comparison (Gondwana Triassic)

Of the group of six genera noted above, *Antevsia*, *Stachyopitys* and *Pteruchus* are most alike in that each bears clusters of similarly elongated microsporangia. Poorly preserved specimens are easily confused. However, *Pteruchus* is differentiated by the clear laminate head bearing numerous abaxial microsporangia; *Stachyopitys* has numerous microsporangia radiating out from a central receptacle; and *Antevsia* has sessile fascicles of microsporangia. The remaining three genera (*Switzianthus*, *Eosteria*, *Kannaskoppianthus*) each display an entirely different organisation.

Reconstructions

Strobilus

Certain reconstructions of the *Pteruchus* strobilus (Crane 1985, p. 755; Retallack & Dilcher 1988, p. 1042) show a dorsiventral structure with the microsporophylls arranged in a single plane. From a study of permineralised specimens of *Pteruchus* from Antarctica, Yao *et al.* (1995) provide a reconstruction that shows helically borne microsporophylls. With some reservation, we believe that the Molteno *Pteruchus* material also has an irregularly helical arrangement as illustrated opposite.

Microsporophyll

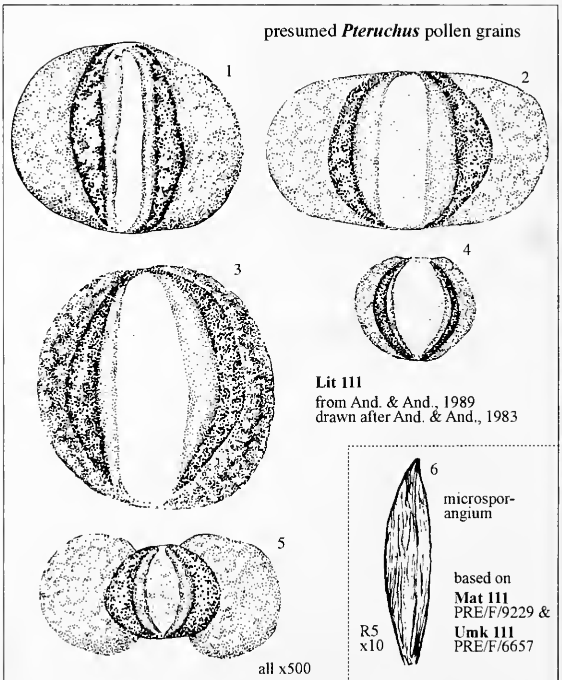
The size of the microsporophyll and whether it is single or paired vary according to species. The marginal lobing of the lamina possibly occurs in all species, but is often obscured by the numerous microsporangia. The lobing was noted by Thomas (1933, p. 234) and Townrow (1962, p. 294, tf. 2E) and is clearly seen in many specimens in our collection, e.g. pl. 94(8, 9).

As shown in our reconstructions of *P. matatimajor* opposite (tfs. 1, 2), a subtending bracteole occurs at the base of each pedicel—clearly seen also in pls 92(9, 11), 93(1, 6). Bracteoles probably occurred on most specimens, but may have been lost before or during preservation. As noted by Townrow (1962, p. 292), who termed them 'vegetative pinnules', they can be quite inconspicuous.

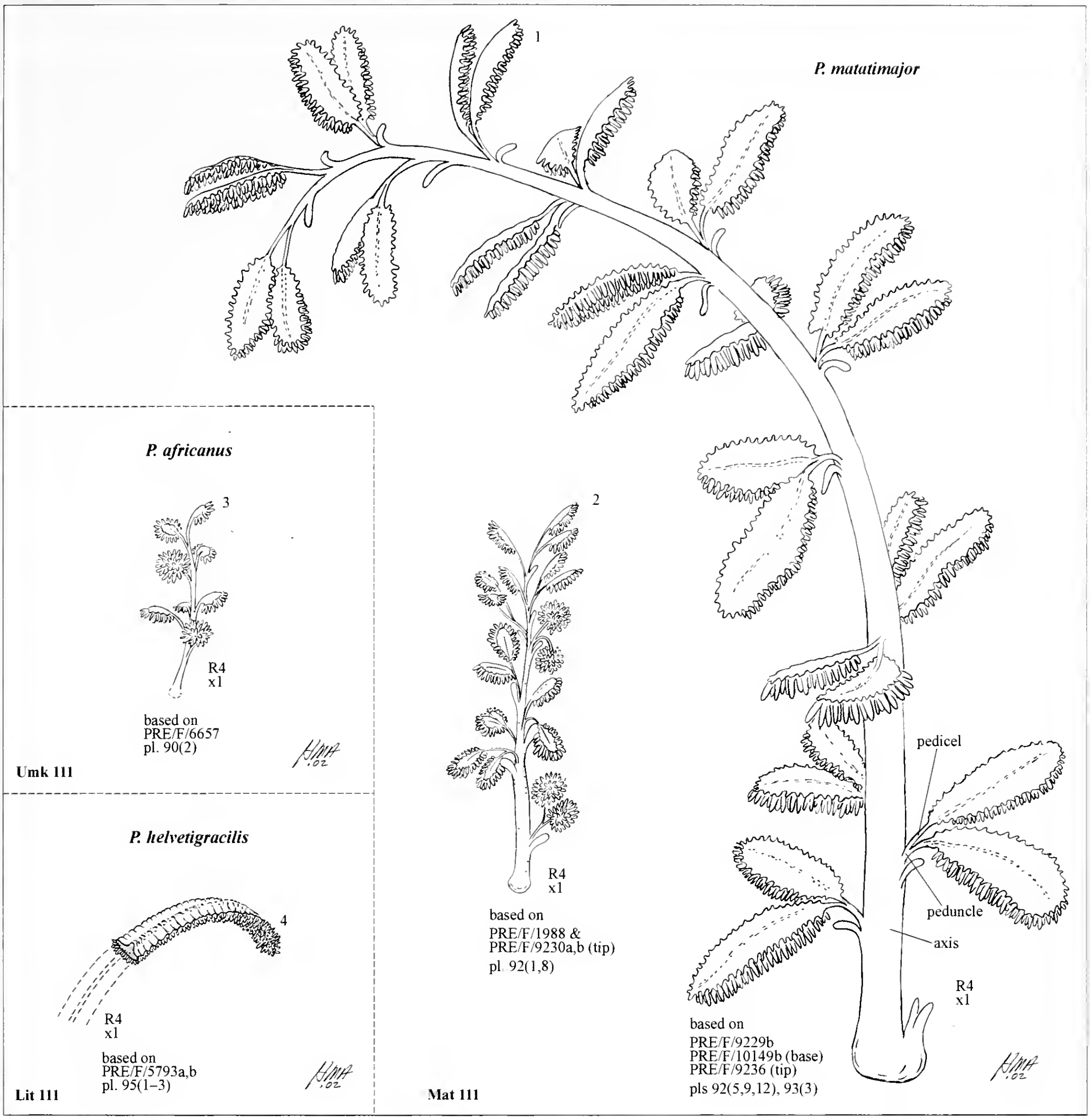
Gondwana Triassic occurrence (elaborated)

Pteruchus, after *Stachyopitys*, is the second most frequent (22 TCs) and abundant (425 indivs) pollen-bearing genus in the Molteno (Tabs 6b, 9b and 11) and the most widely recorded through the Gondwana Triassic. Though *Pteruchus* is now known from all five Gondwana continents (Tab. 53), its true preserved spread and abundance may be strongly under-reported. The most extensive collections come from South Africa (Tab. 54) followed by eastern Australia.

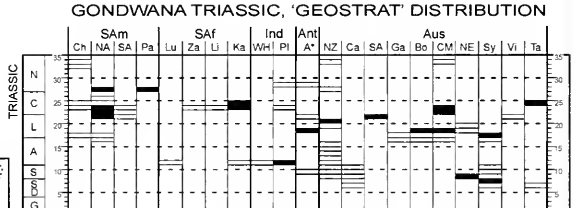
The most widespread species are *P. barrealensis* and *P. feistmantelii*, followed by *P. africanus*. However, most published specimens are insufficiently complete to identify to species level (see Tab. 53, *Pteruchus* hypodigm).

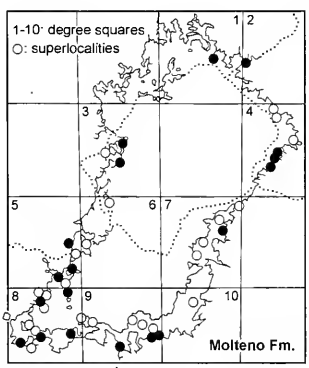


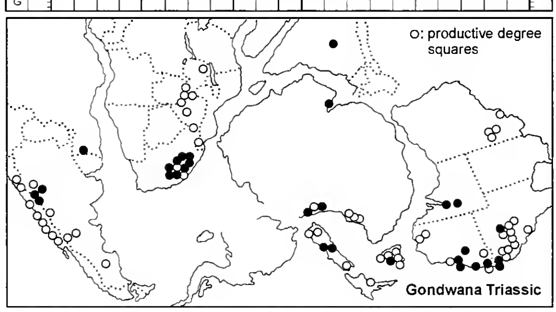
Since a remarkably wide range of *Dicroidium* foliage occurs at Lit 111 (8 distinct palaeodemes, suggesting 8 species; see And. & And., 1983), it is quite possible that all these grains derive from *Pteruchus*—even though only two species of the latter appear to occur in the deposit.



GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION







Tab. 53

PTERUCHUS HYPODIGM, Gondwana Triassic occurrence

	AUTHOR	SUBREGION		FORMATION		LOCALITY	NAME	Indivs	ILLUSTRATION	Species: Molteno			Species: Other			Intactness		
										P. africanus	*P. matatimajor*	*P. helvetigracilis*	*P. barrealen.*	*P. feistmant.*	*P. spp. indet*	Intact strobilus	Fragm. strobilus	Isolated heads
SOUTH AMERICA																		
1876	Geinitz	Marayes	NA3	28	Q. de la Mina	Marayes (Huerta Mts)	*Sphenolepis rhaetica*	2	pl 2(23-24)	-	-	-	-	-	?2	-	1	1
1942	Frenguellli	Barreal	NA2	22	Barreal	Punto II ?	*Pterrorrachis barrealensis*	1	p 2	-	-	-	1	-	-	1	-	-
1944*a*	" (specimen repeated from Frenguelli 1942)						*Zuberia zub. (Pteror. barreal.)*	*	pl 11(1-5)*	-	-	-	*	-	-	*	-	-
1956	Pinto	S. Maria	PA1	28	S. Maria	Passo das Tropas	*Pteruchus*	1	pl 2(3)	-	-	-	-	-	?1	-	1	-
1963+	Bonetti	Barreal	NA2	23	Cortaderita	Punto 32	" *dubius*	1	pl 26	-	-	-	1	-	-	-	1	-
1967	Jain & Del.	Cacheuta	NA 4	24	Potrerillos	Minas de Petroleo	" *rhaetica*	1	pl 90(15)	-	-	-	-	-	-	-	-	1
"	Bort. & Barb. (specimen repeated from Pinto 1956)						*Pteruchus*	*	pl 2(3)*	-	-	-	-	-	*	-	*	-
1980	Petriella (specimen repeated from Frenguelli 1942)						" *dubius var. barreal.*	*	pl 1(1)*	-	-	-	*	-	-	*	-	-
"	" (specimen repeated from Bonetti 1963b)						" " " "	*	pl 1(2)*	-	-	-	*	-	-	-	*	-
"	"	?	?	?	?	?	" " " "	3	pl 1(3-5)	-	-	-	3	-	-	-	-	3
"	"	?	?		?	?	" *simmondsi*	3	pl 2(1-3)	-	-	-	-	-	?3	-	-	3
SOUTH AFRICA																		
1933	Thomas	Underberg	Ka4	24	Molteno	Umkomaas	*Pteruchus africanus*	2	pl 24(71-72), tf 34-35	2	-	-	-	-	-	1	1	-
"	"	"	"	"	"	"	" *papillatus*	1	tf 36-37	1	-	-	-	-	-	1	-	-
"	"	"	"	"	"	"	" *peltatus*	1	tf 38-39	1	-	-	-	-	-	1	-	-
"	"	"	"	"	"	"	" *hoegi*	1	pl 24(75), tf 40-41	1	-	-	-	-	-	1	-	-
"	"	"	"	"	"	"	" *stormbergensis*	1	tf 43	1	-	-	-	-	-	1	-	-
"	"	"	"	"	"	"	" *dubius*	1	tf 44-45	1	-	-	-	-	-	-	-	1
"	"	"	"	"	"	"	" *minor*	1	pl 24(76), tf 46	1	-	-	-	-	-	-	1	-
"	"	"	"	"	"	"	" *sp. Type X*	1	tf 47-48	-	-	-	-	-	-	-	1	-
1962	Townrow						" *africanus*	6	pl 24(4), 25(1,2),	6	-	-	-	-	-	1	1	4
"	"	"	"	"	"	"	" "	-	26(2,4-11), tf 1(A-D,F)	-	-	-	-	-	-	-	-	-
"	"	"	"	"	"	"	" "	-	2(D-G), 3(B-C)	-	-	-	-	-	-	-	-	-
"	"	"	"	"	"	"	" *dubius*	2	pl 24(5,6), 25(3),	2	-	-	-	-	-	1	-	1
"	"	"	"	"	"	"	" "	-	tf 1(E), 4(B,C)	-	-	-	-	-	-	-	-	-
"	"	"	"	"	"	"	" *simmondsi*	1	pl 24(1,3), tf 2(A-C)	1	-	-	-	-	-	1	-	-
"	"	"	"	"	"	"	" "	-	4(A,D-H)	-	-	-	-	-	-	-	-	-
1978–1999: And.& And. Molteno literature not included in this table																		
INDIA																		
1962b	Lele	S. Rewa/Tiki	PL1	12	-	Kamtadand (loc. 9)	*Marattiopsis sp. A*	1	pl 2(16,17) tf 3	-	-	-	?1	-	-	-	-	-
ANTARCTICA																		
1989	Taylor *et al.*	Queen Alexander	TA4	19	Fremouw	Fremouw Peak	*Dicroidium* pollen organs	1	tf 9	-	-	-	-	-	?1	-	-	1
1993	Osb. & Taylor	" "	"	"	"	" "	Corystosperm pollen sacs	1	pl 1	-	-	-	-	-	?1	-	-	1
1995	Yao *et al.*	" "	"	"	"	" "	*Pteruchus fremouwensis*	5	f (1-26)	-	-	-	-	-	?1	-	1	4
1995	Cantrill *et al.*	Pr. Charles Mts	EA1	?	Flagstone Beach	PCM 19	" *dubius*	2	f 5 (a,c)		-	-	-	-	?2	-	-	2
2000	Axsmith *et al.*	Shackleton Gl.	TA6	?	?Fremouw	Alfie's Elbow	*Pteruchus*	2	f 19-29	?2	-	-	-	-	-	2	-	-
NEW ZEALAND																		
1980a	Retallack	Mt Potts	N23	21	Tank Gully CM	Tank Gully	" *johnstonii*	1	f 5A	?1	-	-	-	-	-	-	1	-
1983	"	Benmore Dam	N24	21	Bl. Jack Congl.	Benmore Dam	" *dubius*	1	f 6A	-	-	-	-	-	?1	-	-	1
AUSTRALIA																		
1888	Johnston	Hobart	Ta5	25	Brady equiv.	Lord's Hill (Hobart)	*Baiera tenuifolia*	1	pl 27(2D,E)	?1	-	-	-	-	-	1	-	-
1890b	Feistmantel (specimen repeated from Johnston 1888)						*Trichopitys johnstonii*	*	pl 10(5)*	*	-	-	-	-	-	*	-	-
1898	Shirley	Ipswich/Esk	CM5	24	Blackstone Stage	Denmark Hill	*Stachyopitys annularioides*	1	pl 18(1)	-	-	-	-	-	??1	1	-	-
1925b	Walkom (specimen repeated from Johnston 1888)						" "	*	f 15-16*	*	-	-	-	-	-	*	-	-
1947	Jones & de J.	Ipswich/Esk	CM5	23	Tingalba	Campbell's Quarry	*Pteruchus annulariodes*	1	tf 38	-	-	-	-	-	?1	-	-	1
"	"	"	"	19	Blackstone Stage	Parish Goodna	" *africanus*	1	tf 51	-	-	-	?1	-	-	-	-	-
"	"	"	"	24	Blackstone Stage	Denmark Hill	Strobilus	1	tf 53	-	-	-	-	-	?1	-	-	1
1948	Jones	Bowen Basin	?	?	?	Walhalla, Cracow	Strobilus	1	pl 1(15)	-	-	-	-	-	?1	-	-	1
1962	Townrow (specimen repeated from Johnston 1888)						*Pteruchus johnstonii*	*	tf A-C*	*	-	-	-	-	-	*	-	-
1965	Hill *et al.*	Ipswich/Esk	CM5	24	Blackstone Stage	Denmark Hill	" *dubius*	1	pl T6(3)	-	-	-	?1	-	-	1	-	-
"	"	"	"	24	Blackstone Stage	Denmark Hill	" *johnstonii*	1	pl T6(4)	-	-	-	-	-	1	1	-	-
1973+	Retallack	Blue Mts.	Sy2	8	Banks Wall	Mt. Piddington	*'Pterorrachis' barreal.*	2	pl 16(3), f 17B.	-	-	-	-	2	-	-	2	-
"	"	Sydney	Sy3?	?	?	?	-	7	pl 16(1,2,4-7), f 17(A,D)	-	-	-	-	7	-	-	4	3
1974	Pledge	?Springfield	SA?	22	?	?	*? Pteruchus*	1	pl 7(5)	-	-	-	-	-	?1	-	-	1
1977	Retall. *et al.*	Nymboida	CM7	19	Cloughers Cr.	UNEL 1564	*Pteruchus johnstonii*	1	f 8 (C)	-	-	-	-	-	?1	-	1	-
"	"	"	"	"	"	(Kangaroo Creek)	" *dubius*	1	f 8 (D)	-	-	-	-	-	?1	-	-	1
1979	Holmes & Ash	Lorne B	NE2	9	Camden H. Cl.	Camden Head (1583)	" *barreal. var. feistm.*	3	f 6 (9-11)	-	-	-	-	3	-	-	-	3
1979+	Rowett	Leigh Creek	SA1	-	?	Telford B Lobe B	-	?4	pl 24(1-4)	-	-	-	-	-	?4	-	1	3
1980b	Retallack (specimen repeated from Retallack 1973)						*'Pterorrachis' barreal.*	*	f 21.9(D)*	-	-	-	-	*	-	-	*	*
1981a	"	Sydney	Sy3	?	Newport	?	" "	1	f 10-4(C)	-	-	-	-	1	-	-	1	-
"	"	"	"	?	"	?	*Umkomasia sp.*	1	f 10-4(D)	-	-	-	-	-	?1	-	1	-
1982	Holmes	Dubbo	Sy1	18	(unnamed)	Benolong (Ugothery)	*Pteruchus johnstonii*	2	f 7 (E-F)	2	-	-	-	-	-	2	-	-
"	Playf. *et al.*	Canarvon	Bo5	19	Moolayember	Spring Creek	" *simmondsii*	1	pl 2(5-6)	-	-	-	-	-	?1	-	1	-
1984	Taylor *et al.*	Ipswich/Esk	CM5	?	?	Dinmore	" *dubius*	1	pl 1(1-2)	-	-	-	?1	-	-	1	-	-
1986	White (specimen repeated from Holmes & Ash 1979)						" *barrealensis*	*	ph on p 148 (220)*	-	-	-	-	*	-	-	-	*

+ unpublished
* specimens repeated—number of individuals therefore not given

assemblages (taphocoenosis)	Genera				Species				Intactness		
	Dicroidium	♀ *Umkomasia*	♂ *Pteruchus*	♀ *Fanerotheca*	*P. africanus*	*P. matatimajor*	*P. helvetigracilis*	*P.* spp indet	Intact strobili	Partial "	Isolated heads
Ken 111 Dic cra	**99**	-	-	-	-	-	-	-	-	-	-
Nav 111 Dic odo	**98**	-	-	1	-	-	-	-	-	-	-
Cal 111 Dic/Sph	**50**	-	-	-	-	-	-	-	-	-	-
Bir 211 Sph 2spp	**4**	-	-	1	-	-	-	-	-	-	-
" 311 Hei/Sph	**14**	2	1	2	-	-	-	1	-	-	1
Bir 111 " "	**1**	-	-	60	-	-	-	-	-	-	-
Gre 121 Hei elo	3	-	-	-	-	-	-	-	-	-	-
" 111 Equ sp.	**2**	-	-	3	-	-	-	-	-	-	-
Boe 111 Lep sto	5	-	-	1	-	-	-	-	-	-	-
" " Dic/Hei	**56**	-	-	-	-	-	-	-	-	-	-
" 112 Dic cor	**99**	8	10	-	10	-	-	-	-	5	5
Cyp 111 Dic cra	**75**	2	-	1	-	-	-	-	-	-	-
Mol 111 Sph pon	**12**	-	-	1	-	-	-	-	-	-	-
Kan 112 Hei elo	**1**	-	-	-	-	-	-	-	-	-	-
Tel 111 " "	**6**	-	1	2	-	-	-	-	-	-	1
Kom 111 Sph/Dic	**39**	-	-	2	-	-	-	-	-	-	-
Vin 111 Dic odo	**70**	-	-	-	-	-	-	-	-	-	-
Ela 111 " "	**87**	1	3	1	3	-	-	-	-	1	2
Kra 311 " "	**99**	-	-	-	-	-	-	-	-	-	-
" 221 Beetles	**50**	-	-	-	-	-	-	-	-	-	-
" 111 Dic odo	**90**	14	30	-	30	-	-	-	-	11	19
Lut 111 Hei/Dic	**40**	-	-	-	-	-	-	-	-	-	-
" 411 " "	**50**	-	-	-	-	-	-	-	-	-	-
" 311 Hei elo	58	-	-	7	-	-	-	-	-	-	-
" 221 Equ sp.	**1**	-	-	-	-	-	-	-	-	-	-
Tin 121 Sph 2spp	**1**	-	-	1	-	-	-	-	-	-	-
Wal 111 Dic odo	**92**	-	-	24	-	-	-	-	-	-	-
Kon 223 " "	**80**	-	-	-	-	-	-	-	-	-	-
" 222 " "	**87**	22	13	1	9	3	-	1	-	9	4
" 211 Hei elo	**5**	-	-	-	-	-	-	-	-	-	-
" 111 Dic odo	**78**	-	1	-	1	-	-	-	-	-	1
" " Hei elo	3	-	-	-	-	-	-	-	-	-	-
Pen 321 Dic/Ris	**51**	-	-	-	-	-	-	-	-	-	-
" 211 Dic/Equ	**50**	-	-	-	-	-	-	-	-	-	-
" 221 " "	**40**	-	-	-	-	-	-	-	-	-	-
" 511 Equ sp.	**2**	-	-	-	-	-	-	-	-	-	-
" 421 Dic odo	**89**	-	-	-	-	-	-	-	-	-	-
" 431 Dic/Equ	**40**	-	-	-	-	-	-	-	-	-	-
" 311 Hei elo	**25**	3	4	-	4	-	-	-	-	-	4
" 411 " "	13	-	-	-	-	-	-	-	-	-	-
Kle 111 Hei/Dic	**45**	-	-	1	-	-	-	-	-	-	-
Kap 111 Dic/Ris	**50**	2	11	40	11	-	-	-	2	5	4
Ela 112 Equ sp.	**1**	-	-	-	-	-	-	-	-	-	-
" " Dic/Hei	**60**	-	-	2	-	-	-	-	-	-	-
Nuw 111 Dic zub	**70**	11	15	-	15	-	-	-	-	6	9
" 211 Dic 2spp	**98**	-	-	-	-	-	-	-	-	-	-
Win 111 Hei elo	**10**	-	-	-	-	-	-	-	-	-	-
Mor 111 Dic zub	**99**	-	-	-	-	-	-	-	-	-	-
" " Dic odo	**98**	3	1	-	1	-	-	-	-	-	1
Qua 111 Dic odo	**40**	1	-	-	-	-	-	-	-	-	-
Mak 111 " "	**90**	-	-	-	-	-	-	-	-	-	-
Maz 111 Dic cra	**74**	-	-	6	-	-	-	-	-	-	-
" 211 Hei/Dic	**64**	46	27	5	27	-	-	-	9	15	3
Moo 111 Dic zub	**99**	-	-	-	-	-	-	-	-	-	-
Hla 111 Equ sp.	**1**	-	-	-	-	-	-	-	-	-	-
" 211 Dic 3spp	**85**	3	2	3	2	-	-	-	1	1	-
" 212 " "	**91**	4	4	-	4	-	-	-	1	1	2
" 213 Dic elo	**89**	32	20	5	17	1	-	2	3	11	6
Umk 111 Dic 2spp	**80**	197	138	16	138	-	-	-	34	64	40
Cha 111 Dic odo	**100**	-	-	-	-	-	-	-	-	-	-
" 211 Dic dub	**80**	-	-	-	-	-	-	-	-	-	-
Inj 111 Dic odo	**100**	-	-	-	-	-	-	-	-	-	-
" 211 Dic dub	**90**	-	-	-	-	-	-	-	-	-	-
San 111 Dic cra	**90**	4	5	5	5	-	-	-	-	2	3
Mng 111 Dic 2spp	**93**	-	-	-	-	-	-	-	-	-	-
Qac 111 Hei/Dic	**50**	-	-	-	-	-	-	-	-	-	-
Mat 111 Dic dub	**89**	75	84	6	-	84	-	-	15	34	35
Gol 111 " "	**99**	1	1	-	1	-	-	-	1	-	-
Lit 111 Dic/Hei	**50**	51	36	3	33	-	3	-	3	19	14
Aas 111 Hei elo	7	-	-	-	-	-	-	-	-	-	-
" 311 " "	15	-	-	-	-	-	-	-	-	-	-
" 411 c/Sph	**60**	7	3	47	-	3	-	-	1	-	2
" 511 Dic elo	**60**	-	-	-	-	-	-	-	-	-	-
Ask 111 Equ sp.	**21**	14	15	-	15	-	-	-	-	5	10
Bam 111 Dic dub	**98**	-	-	-	-	-	-	-	-	-	-
Total TCs	75	22	22	27	17	4	1	3	10	15	21
Total indivs	%	503	425	247	327	91	3	4	70	189	166

Tab. 54. *Pteruchus*, Molteno occurrence

Comparisons beyond Gondwana Triassic

Laurasia Triassic

Besides *Stachyopitys* and *Antevsia*, no other genera with a closely similar structure to *Pteruchus* are known to us.

Pteruchus septentrionalis, together with the doubtful *Umkomasia franconia* (p. 243), has been described by Kirchner & Müller (1992) from the Bayreuth area (Grossbellhofen and Unternschreez), Germany. The *Pteruchus* specimen illustrated by them on pl. 3(4) is possibly close to *Pteruchus*, while that on pl. 3(2) is something very different. We do not accept these as *Pteruchus* and suggest that they belong to a new genus affiliated to *Thinnfeldia* to which they are clearly linked by the similar cuticle structure.

Other ages

Certain male strobili from the Carboniferous, e.g. *Crossotheca* and *Feracotheca* (order Lagenostomales), bear numerous abaxial microsporangia and in this way show similarities to *Pteruchus* (see Taylor & Taylor 1993).

Evidence for affiliation of organs

The female/male balance in occurrence (Molteno Fm.)

The pattern of occurrence of the female and male strobili affiliating with *Dicroidium* is quite unique. It is the only case, for the 20 gymnosperm ovulate genera recognised within the Molteno, where the pattern of distribution (presence and abundance) of the affiliated organs appears closely parallel. This parallelism of occurrence shows very clearly in Tabs 52, 54. *Umkomasia* and *Pteruchus* each occur in 22 TCs, and appear together in similar abundance in most cases (in 20 TCs).

In marked contrast, a strong imbalance in preservation between male and female organs is the normal pattern: *Dordrechtites* and *Fraxinopsis*, for instance, are frequent and abundant, but for neither is there any evident male counterpart; *Telemachus* and *Peltaspermum* are very much more frequent and abundant than their male affiliates, *Odyssianthus* and *Antevsia*, respectively; *Rissikistrobus* and *Rissikianthus*, female and male cones of *Rissikia*, generally co-occur but either the one or the other is distinctly more abundant; in *Kannaskoppia*, where the reverse to the general pattern is observed, the male strobilus far outstrips the female in frequency; and lastly, in a few cases, male cones occur without any apparent female counterpart.

Why is the *Umkomasia*/*Pteruchus* pattern unique? What is there about the *Dicroidium* plant that makes it different from all other Molteno gymnosperms in this regard? Why should it be the only case where the effect of taphonomic filtering appears to be so strikingly similar for female and male? We need, perhaps, to look at the other unique facts about *Dicroidium*. It is by far the most prominent/successful gymnosperm genus in Gondwana with regard to the combination of ubiquity, frequency, abundance and diversity (And. & And. 1989; pp. 46, 68). It is the dominant genus in three of the seven recognised Molteno habitats (Cairncross *et al.* 1995): *Dicroidium* riparian forest (mature and immature) and the *Dicroidium* open woodland of the floodplain. Is the explanation behind its success in some way related to that behind its uniquely parallel female/male pattern of occurrence?

Adaptive radiation (Molteno diversity)

The numerous species described by Thomas (1933) and Townrow (1962) from Umk 111 (Umkomaas Valley) are all considered to be *P. africanus* (see *Pteruchus* hypodigm, Tab. 53).

While 19 species of *Dicroidium* and eight species of *Umkomasia*—the well-established foliage and female affiliates of *Pteruchus* respectively—are recognised for the Molteno, only three species of *Pteruchus* can be readily differentiated. The diagnostic characters of *Pteruchus* lie primarily in the shape and size of the fertile heads, the nature of the lamina margin, and whether or not the pedicels are forked.

The three species, each based on substantial palaeodemes from a different TC (all from the Indwe Member) and derived from *Dicroidium* riparian forest habitats, are:

P. africanus—Umk 111 Dic 2 spp (Umkomaas Valley), 138 indivs
Dicroidium riparian forest (mature); Cycle 2b (Indwe Member)
P. matatimajor—Mat 111 Dic dub (Matatiele), 84 indivs
Dicroidium riparian forest (immature); Cycle 2b (Indwe Member)
P. helvetigracilis—Lit 111 Dic Hei (Little Switzerland), 3 indivs
Dicroidium riparian forest (immature); Cycle 2a (Indwe Member)

Pteruchus africanus H.H.Thomas 1933

Holotype
Specimen: V23384 (U244), Nat. Hist. Mus., London.
Thomas (1933), fig. 34, pl. 24 (71); refigured here, p. 255, tf. 4.
Assemblage (TC): Umk 111 Dic 2spp; Umkomaas Valley.
Preservation: an intact strobilus, compression in thinly laminated, carbonaceous (good cuticle), moderately baked, dark grey shale with good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 138 indivs (34 intact, 64 partial, 40 isolated), pl. 90(1–9).

Sister palaeodemes—16 (best 2 listed)
Hla 213 Dic elo: 17 indivs (2 intact, 9 partial, 6 isolated), pl. 91(1–6).
Kra 111 Dic elo: 30 indivs (11 partial, 19 isolated).

Specific diagnosis
A *Pteruchus* species with small strobili, bearing unforked microsporophylls with oval fertile heads and relatively robust microsporangia.

Specific characters
Strobilus: small (*ca* 30–40 mm long).
Microsporophyll: peduncle unforked.
Fertile head: oval (*ca* 5–10 mm long).
Microsporangium: relatively robust.

Etymology
africanus—named by Thomas (1933) as coming from Africa.

Comment & comparison
Though there is some apparent morphological overlap between this species and *P. matatimajor* at the smaller end of the latter's range, the two species are clearly distinct. The full collection of 138 *Pteruchus* specimens from Umk 111 constitutes a single palaeodeme of small strobili with small, unpaired, circular to oval microsporangial heads.

Pteruchus matatimajor J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/9229a,b; pl. 92(5, 12).
Assemblage (TC): Mat 111 Dic dub, Matatiele.
Preservation: central part of strobilus with tip and base missing, part and counterpart; impression in thickly laminated, olive-grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 84 indivs (15 intact, 34 partial, 35 isolated), pls 92–94.

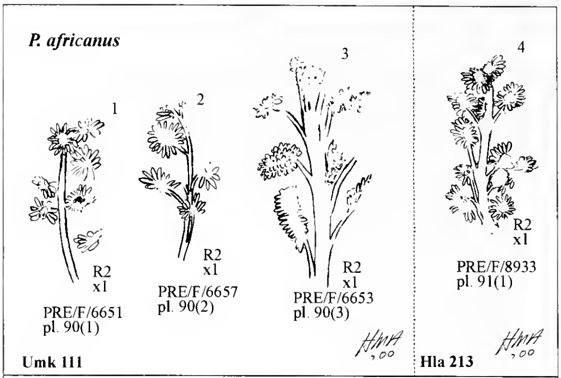
Sister palaeodemes—3 (all listed)
Hla 213 Dic elo: 1 indiv. (1 intact), pl. 91(7–10).
Kon 222 Dic odo: 3 indivs (3 partial).
Aas 411 Dic/Sph: 3 indivs (1 intact, 2 isolated).

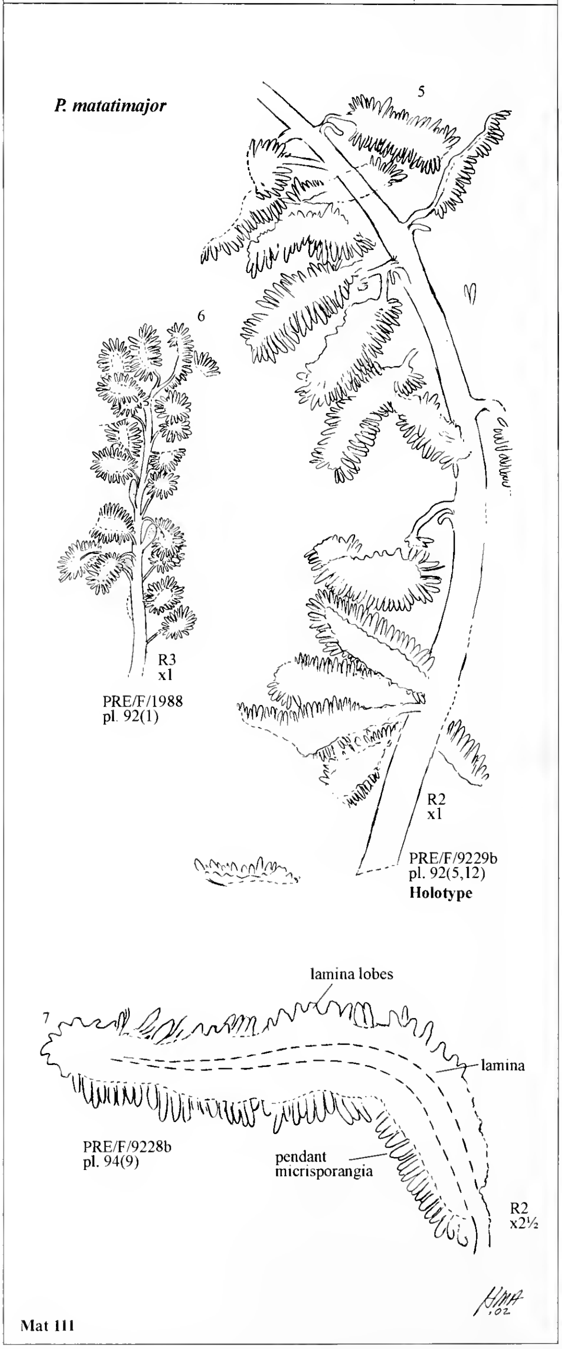
Specific diagnosis
A *Pteruchus* species with medium to large strobili, bearing forked microsporophylls with oblong to linear-oblong fertile heads and relatively robust microsporangia borne on deeply lobed leafy laminae.

Specific characters
Strobilus: medium to large (*ca* 45–>120 mm long).
Microsporophyll: peduncle normally once forked.
Fertile head: oblong to linear-oblong (5–25 mm long); leafy lamina with deeply defined lobes.
Microsporangium: relatively robust.

Etymology
matatimajor—with reference to the large size of the specimens from the Matatiele locality.

Comment & comparison
The large Mat 111 *Pteruchus* collection of 84 individuals covers a wide range of variation in size, yet appears to constitute a single palaeodeme characterised by the consistently forked microsporophylls and linear-oblong fertile heads. Particularly distinctive are the laminae with their coarse, clear lobing [pl. 94(8, 9)].





Pteruchus helvetigracilis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: BP/2/5793a,b; pl. 95(1–3, 5–7).
Assemblage (TC): Lit 111 Dic Hei, Little Switzerland.
Preservation: an incomplete microsporophyll, part and counterpart; compression in thinly laminated, carbonaceous (good cuticle), dark grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 3 indivs (3 isolated), pl. 95(1–7).

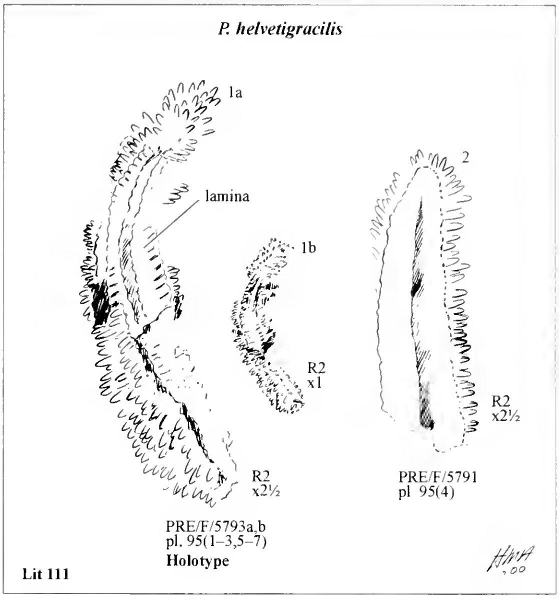
Sister palaeodemes—nil.

Specific diagnosis
A *Pteruchus* species of unknown size, bearing microsporophylls with linear fertile heads and relatively gracile microsporangia.

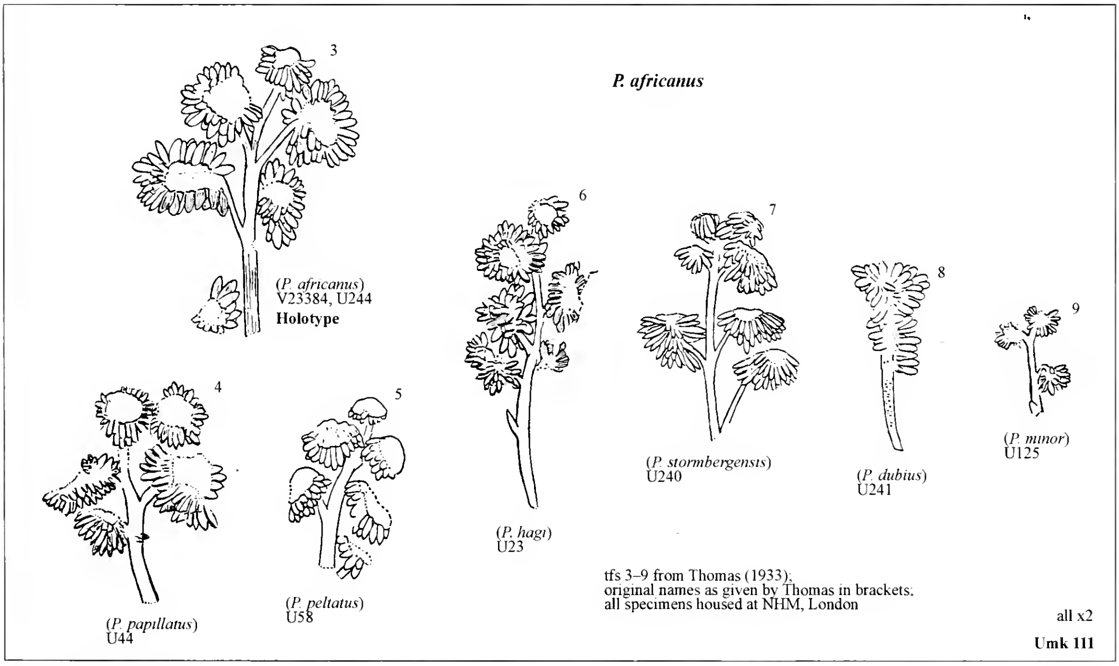
Specific characters
Strobilus: unknown.
Microsporophyll: peduncle unknown.
Fertile head: linear (>30 mm long), margins of leafy lamina uncertain.
Microsporangium: relatively gracile.

Etymology
helvetigracilis—helveti (Lat.), Switzerland, referring to the type locality Little Switzerland; *gracilis* (Lat.), slender, referring to the form of the microsporangia.

Comment & comparison
With only three incomplete microsporangial heads from Lit 111, this is by far the rarest and most infrequent of the Molteno *Pteruchus* species. It could possibly be included with *P. matatimajor*, both seemingly affiliated with *Dicroidium zuberi*, but does appear distinctly more gracile in all respects.



Cuticles
Potential sample: Lit 111, 36 indivs; Umk 111, 138 indivs.
Macerated: none in this work; see Thomas (1933) and Townrow (1962).
Preservation grade: Grade 4–5.
Diagnostic characters: cells isodiametric to linear-oblong, end walls square to oblique, walls gently curved to sinuous, nonpapillate to papillate; trichome bases present; stoma orientation (?)random; subsidiary cells brachyparacytic and actinocytic, nonlappetate; guard cells narrowly elliptic.
Comment: —
Significance:
Classification—The cuticles of *Pteruchus*, as described and illustrated by Thomas (1933) and Townrow (1962), are closely similar to those of *Umkomasia* (in Thomas 1933) and *Dicroidium* (in And. & And. 1983, 1989)—thus supporting classification in the order Umkomasiales.
Affiliations—As noted for *Umkomasia* (p. 240), and for the same reasons, the cuticle of *Pteruchus* clearly supports affiliation with *Dicroidium* rather than the other Molteno ginkgoopsid foliage genera *Lepidopteris*, *Sphenobaiera*, *Ginkgoites* and *Dejerseya*.



Dicroidium Gothan 1912

Type species
Dicroidium odontopteroides (Morris 1845) Gothan 1912.
Jerusalem Basin, Tasmania; Carnian, Triassic.

Generic diagnosis
A Y-shaped ginkgoopsid leaf with a short distinct petiole and simple to tripinnate lamina with lateral venation arching and forking.

Generic characters
Sterile shoot: with terminally attached fascicles of 2–5 or more leaves.
Leaf: Y-shaped, medium to large, *ca* 200–300 (up to 1000 mm) long; rhachis dichotomising about a third from base; lamina entire to tripinnate; petiole short; pinnae contracted or rarely decurrent at base, highly variable in shape; venation varying with pinna shape from taenioptera to odontopteroid with veins arching and forking once or twice.
Cuticle: see And. & And. (1989, p. 69); this vol., tfs 5a–c.

Etymology
Dicroidium—dichro, dikros (Gr.), forked; *idium* (Lat.), a suffix indicating diminutiveness.

Global range: 21 spp., Gondwana, Tr. (SCY–NOR).
First: *Dicroidium zuberi* (*Thinnfeldia odontopteroides*) (Feistmantel, 1890); Banks Wall Fm., Mt. Piddington, Blue Mts, Australia.
Last: *Dicroidium odontopteroides* (*Thinnfeldia lancifolia*) (Solms-Laubach & Steinmann 1899); Quebr. La Ternera, Copiapo, Chile.

Gondwana Triassic occurrence
Frequency (F): 45 degree squares (of the 84 across Gondwana).
Ubiquity (U): 5 continents (of 5 comprising Gondwana).
Diversity (D): 21 species.
Abundance (A): 90% (the norm in preferred Molteno habitats).
Longevity (L): 27 myrs (Smithian to late Norian).

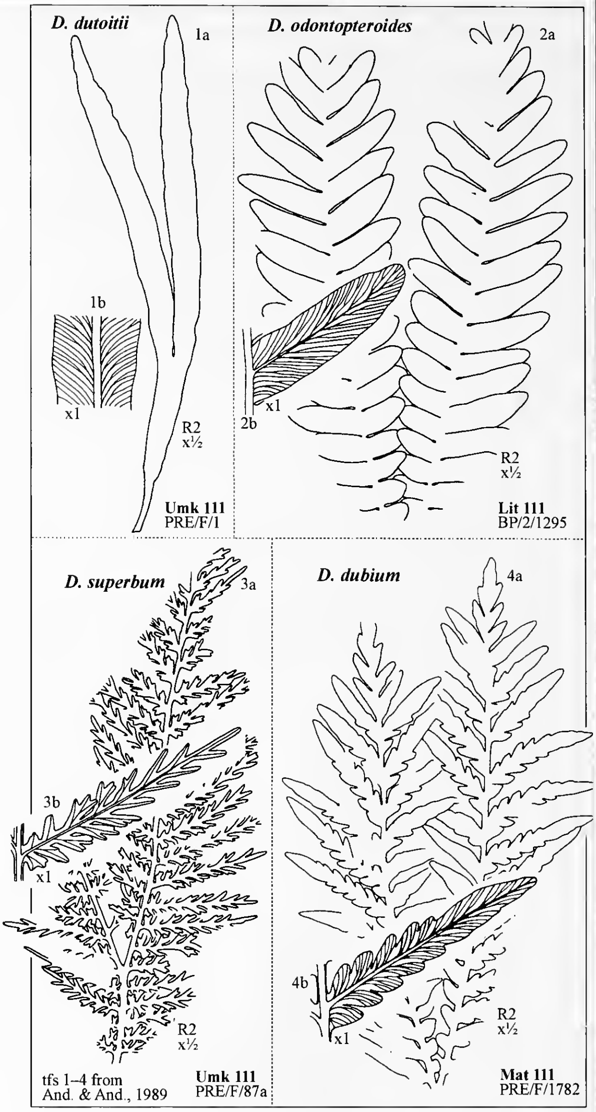
Colonisation success: FUDAL rating 45/5/21/90/27 = 188.
Maximum success (Grade 5); *Dicroidium* was clearly the most prominent genus in the Gondwana Triassic; it was ubiquitous, frequent, diverse, abundant and long-lived.
Endemism: many of the *Dicroidium* species and infraspecific taxa colonised widely across Gondwana.

Molteno occurrence
Frequency (F): 75 TCs (of 100 sampled in the Molteno).
Diversity (D): 21 species.
Abundance (A): monodominant (>70%) in 32 TCs; co-dominant (20–69%) in 23 TCs; occasional to abundant (1–19%) in 12 TCs; rare to very rare (<1%) in 8 TCs.

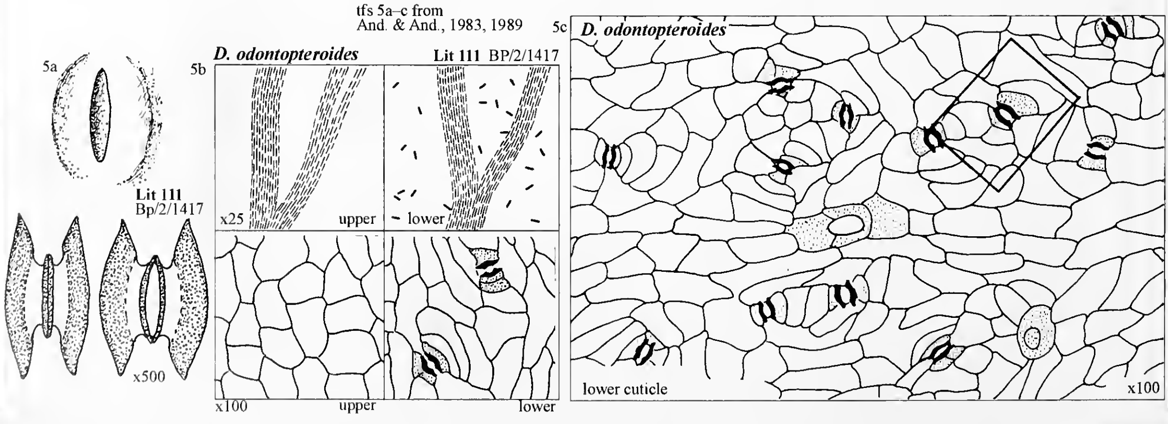
Habit: woody, probably from shrubs to large canopy trees.
Preferred habitat: the dominant genus in 3 of the 7 primary Molteno habitats—*Dicroidium* riparian forest (types 1 and 2) and *Dicroidium* woodland.

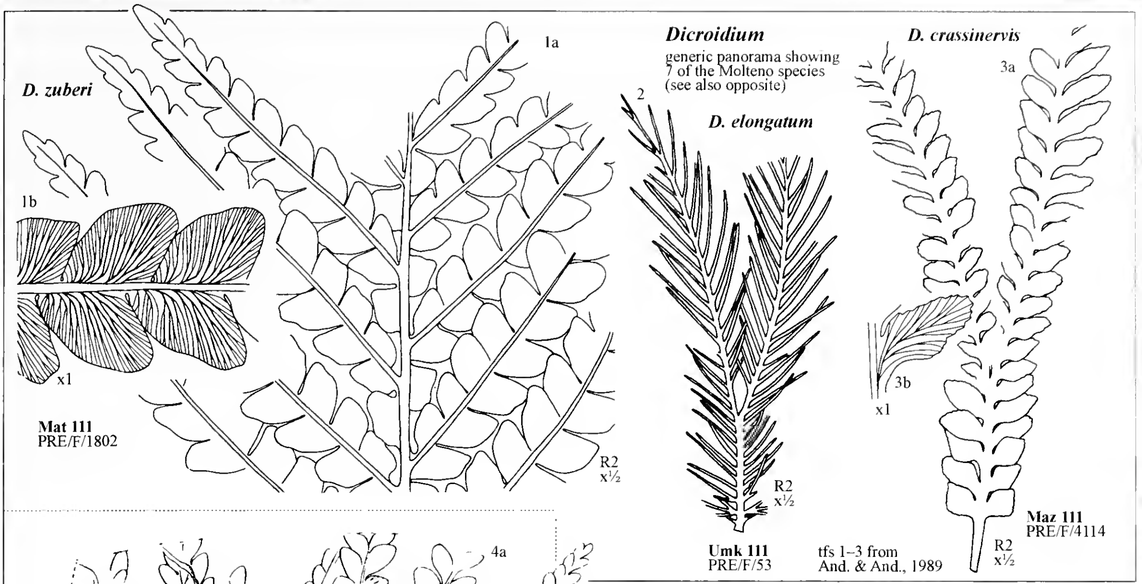
Affiliated organs
Female strobilus: *Umkomasia*—Grade 4 (Mut. occ., Cut. corr.).
Male strobilus: *Pteruchus*—Grade 4 (Mut. occ., Cut. corr.).

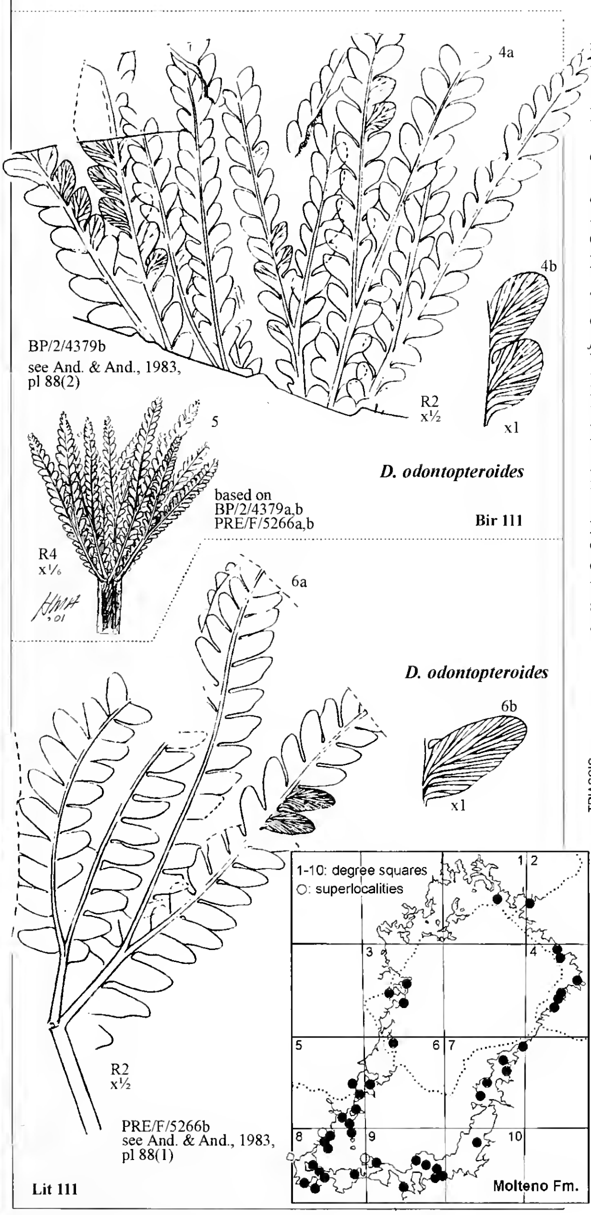
Classification & comparison
See And. & And. (1989, p. 68).



Adaptive radiation (diversity)
Dicroidium, a well-defined genus, is particularly diverse at the species and infraspecific level. It is primarily in the shape of the pinnae and pinnules that the different taxa are recognised. Evidence suggests that the *Umkomasia/Dicroidium* plant-genus actively colonised and diversified through much of the Triassic. A reticulate, rather than punctuate, model of speciation is conceived (And. & And. 1983, 1989). We currently recognise 21 species Gondwana-wide (see p. 22).







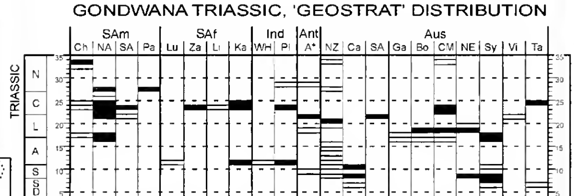
Leaf attachment

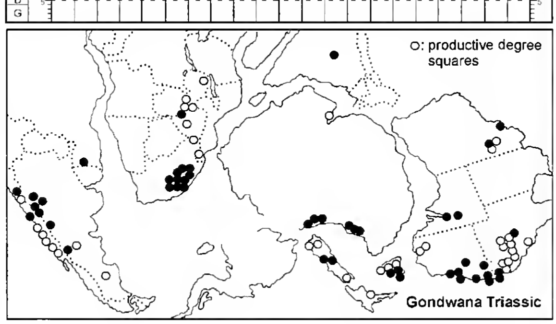
Although *Dicroidium* foliage is so abundant throughout Gondwana, only one pair of attached leaves (tf. 6a) from the Molteno [And. & And. 1983, pl. 88(1)] and one single attached leaf from Antarctica (Axsmith *et al.* 2000) have been reported. A third specimen of importance (tf. 4a) shows a group of five leaves (and fragments of a further two) arranged in a fascicle but with their base and point of attachment missing [And. & And. 1983, pl. 88(2)].

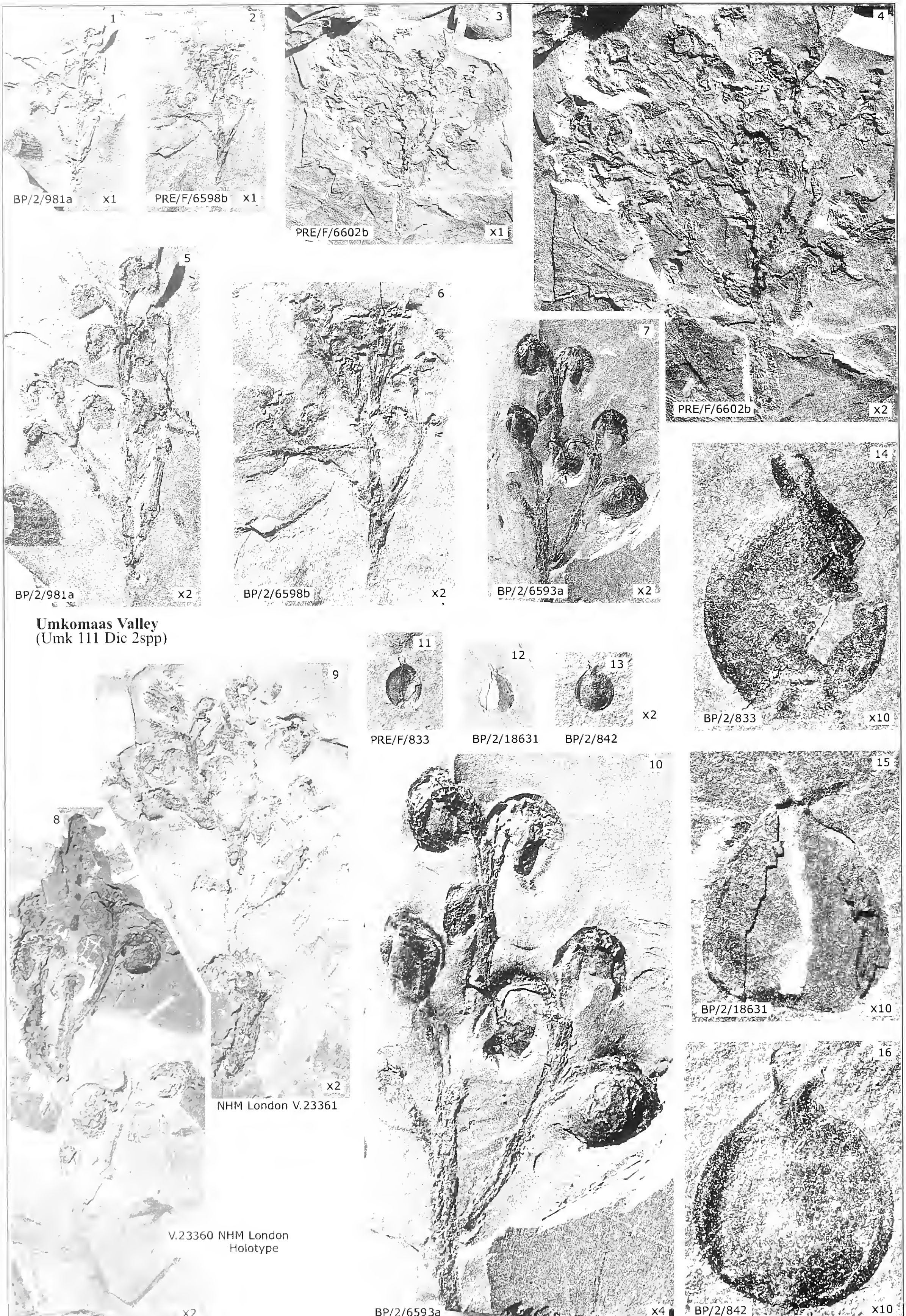
Based on the structural similarity of petrified material from the Middle Triassic Fremouw Fm., Antarctica, Meyer-Berthaud *et al.* (1993) suggested that the small stems/twigs they described as *Kykloxylon* bore *Dicroidium fremouwensis* Pigg (1990) leaves. The latter derive from the same locality but have not been found in organic connection. From the orientation of the leaf bases they suggest that the 'distal-most twigs bear helically arranged leaves'. Considering the Lit 111 specimen (tf. 6a), which shows two leaves attached at the end of a 40 mm length of slender twig (0.5 mm diam.), and the group of leaves from Bir 111 (tf. 4a), a terminal leaf fascicle is suggested. This could be accommodated by a close helical phyllotaxy as drawn in the reconstruction tf. 5.

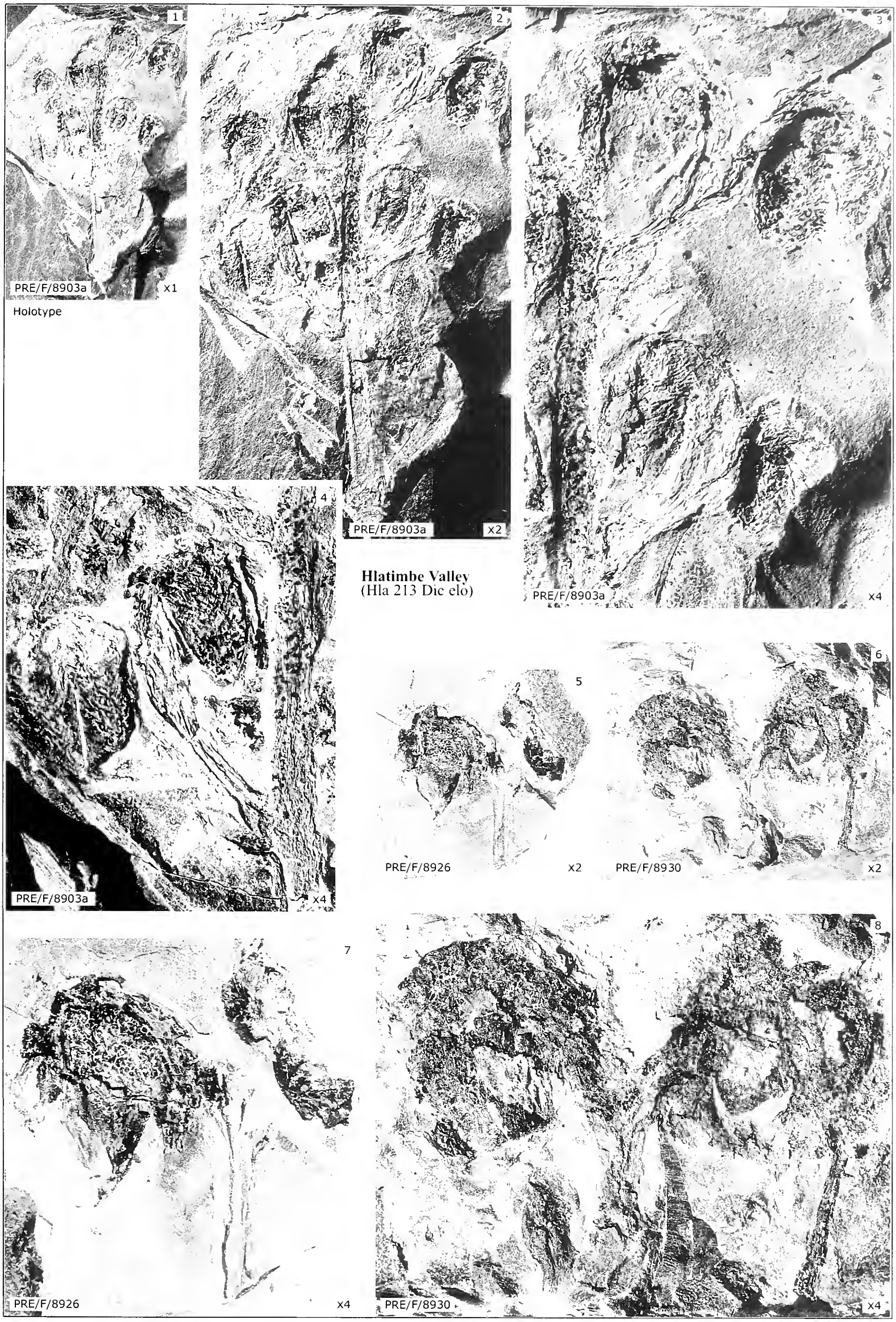
The single *Dicroidium* leaf from Antarctica (Axsmith *et al.* 2000) is problematic in that it appears to be attached to a robust axis (*ca* 15 mm in diameter) and not to one of the short shoots borne by this same axis. In extant plants with long and short shoots, the leaves are not directly attached to mature shoots; e.g. in *Ginkgo biloba*, leaves occur in fascicles on short shoots or as individual leaves on long shoots which typically have a thin axis.

GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION

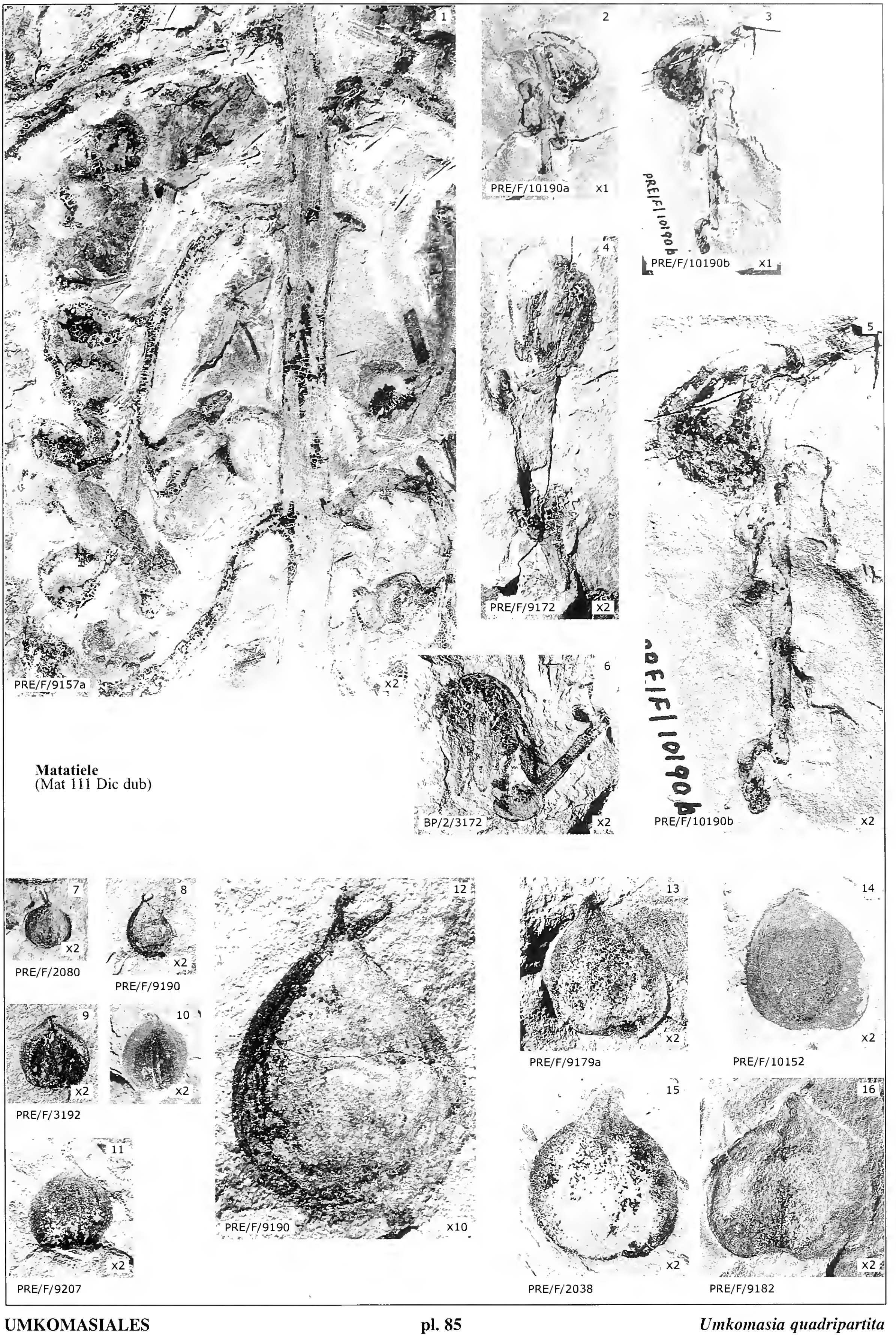


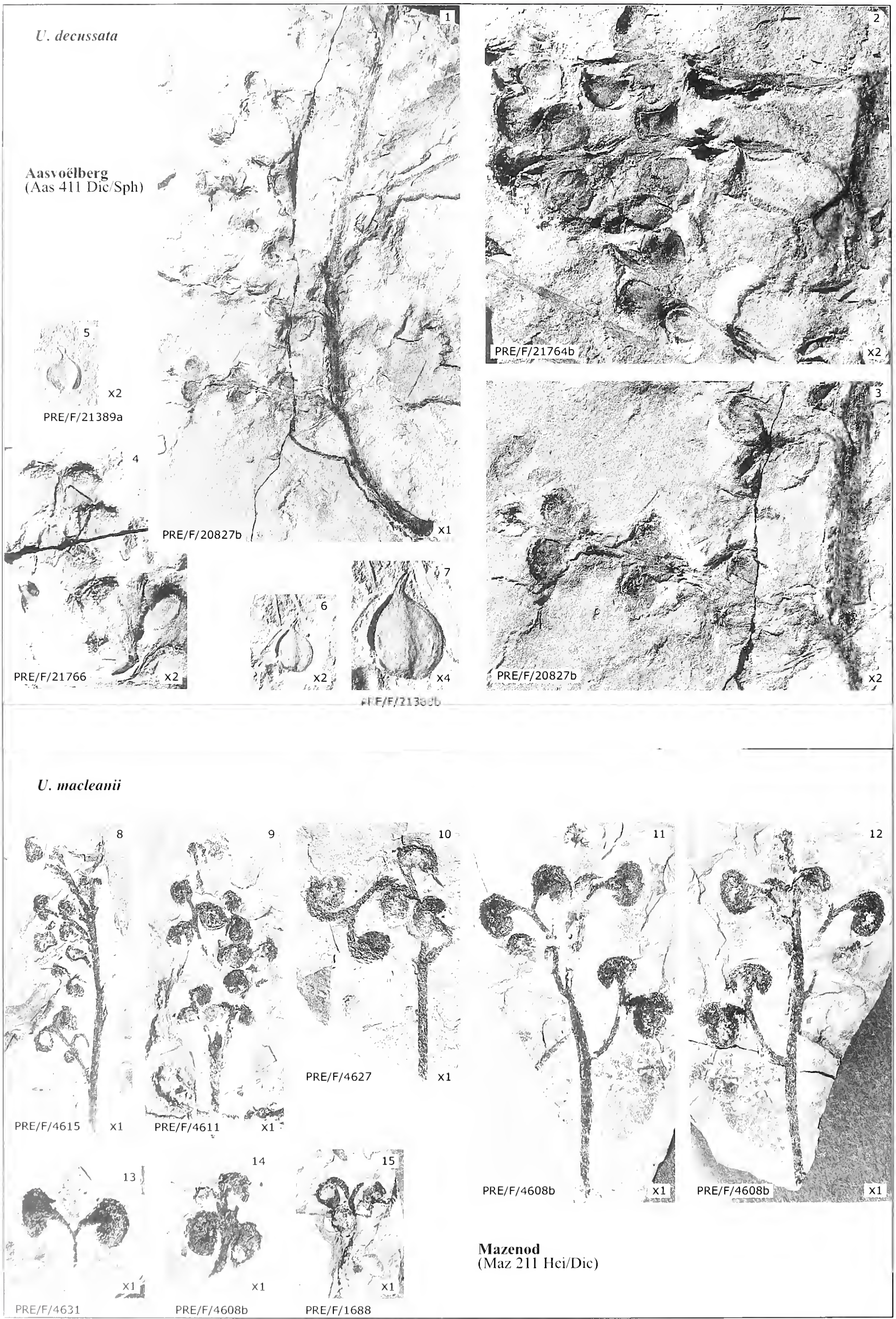



1
2
3
4
BP/2/981a x1
PRE/F/6598b x1
PRE/F/6602b x1
5
6
7
PRE/F/6602b x2
14
BP/2/981a x2
BP/2/6598b x2
BP/2/6593a x2
Umkomaas Valley
(Umk 111 Dic 2spp)
11
12
13
9
x2
PRE/F/833
BP/2/18631
BP/2/842
BP/2/833 x10
10
15
8
BP/2/18631 x10
x2
NHM London V.23361
16
V.23360 NHM London
Holotype
x2
BP/2/6593a x4
BP/2/842 x10

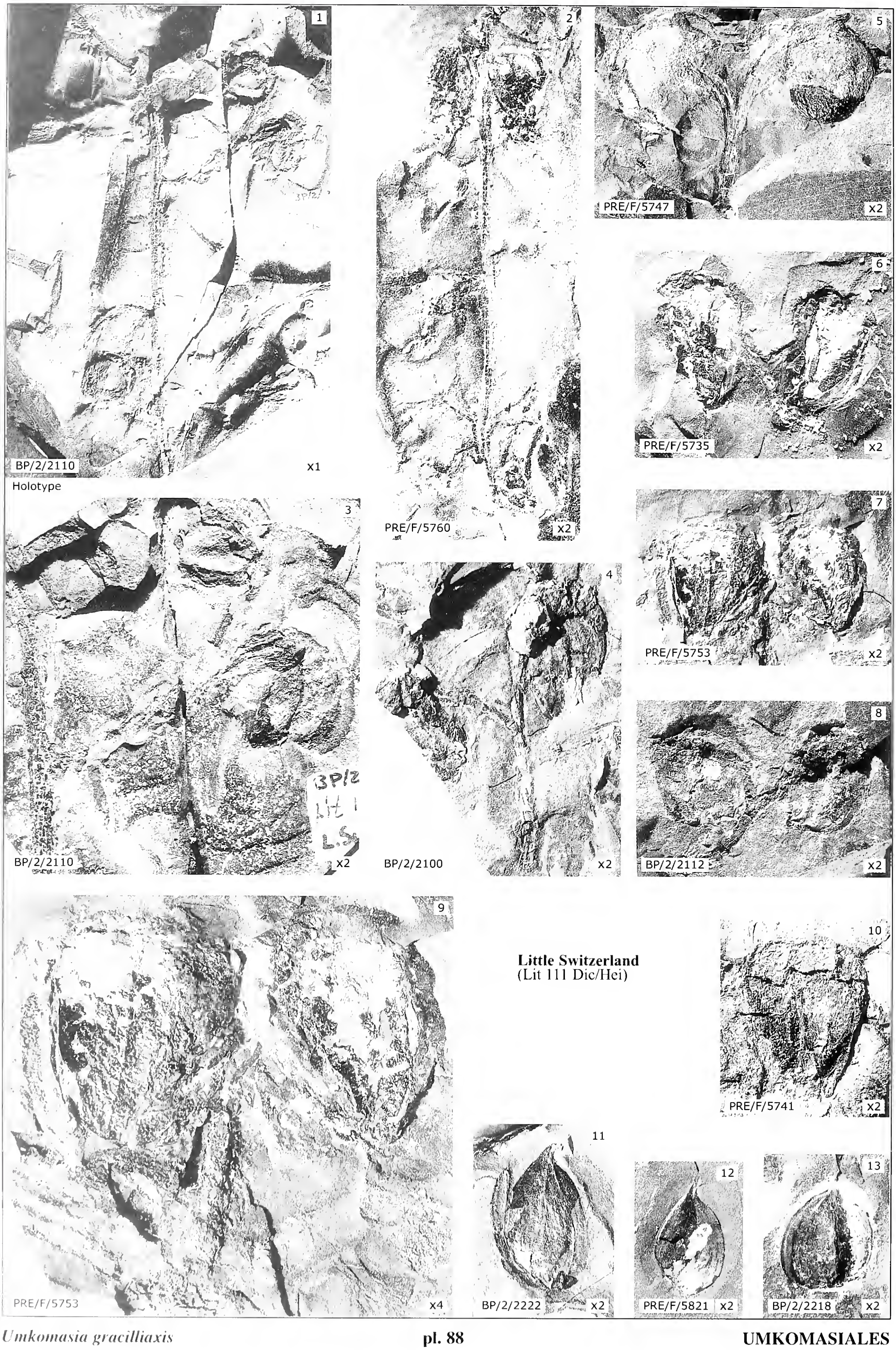

1
PRE/F/8903a
x1
Holotype
2
PRE/F/8903a
x2
3
PRE/F/8903a
x4
Hlatimbe Valley
(Hla 213 Dic elo)
4
PRE/F/8903a
x4
5
PRE/F/8926
x2
6
PRE/F/8930
x2
7
PRE/F/8926
x4
8
PRE/F/8930
x4


1
PRE/F/9157a
x1
Holotype
2
PRE/F/9152a
x1
3
BP/2/3155a
x1
Matatiele
(Mat 111 Dic dub)
4
PRE/F/9158a
x1
5
PRE/F/9157a
x2


1
PRE/F/9157a
x2
2
PRE/F/10190a
x1
3
PRE/F/10190b
x1
4
PRE/F/9172
x2
5
PRE/F/10190b
x2
6
BP/2/3172
x2
Matatiele
(Mat 111 Dic dub)
7
x2
PRE/F/2080
8
x2
PRE/F/9190
9
x2
10
x2
PRE/F/3192
11
x2
PRE/F/9207
12
PRE/F/9190
x10
13
x2
PRE/F/9179a
14
x2
PRE/F/10152
15
x2
PRE/F/2038
16
x2
PRE/F/9182

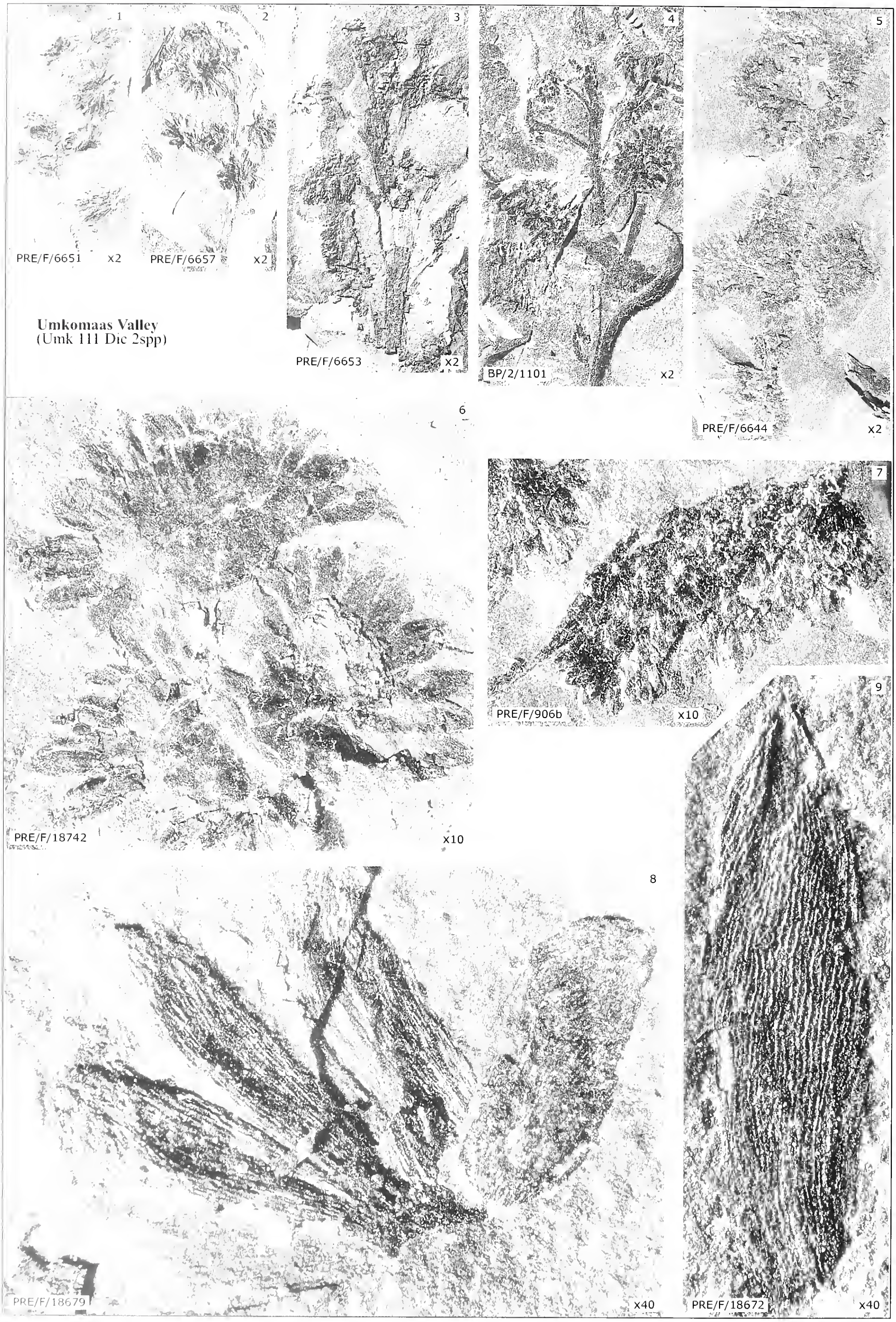

U. decussata
1
2
Aasvoëlberg
(Aas 411 Dic/Sph)
5
x2
PRE/F/21389a
PRE/F/21764b
x2
3
4
PRE/F/20827b
x1
6
7
PRE/F/21766
x2
x2
x4
PRE/F/20827b
x2
PRE/F/21388b
U. macleanii
8
9
10
11
12
PRE/F/4627
x1
PRE/F/4615
x1
PRE/F/4611
x1
13
14
15
PRE/F/4608b
x1
PRE/F/4608b
x1
Mazenod
(Maz 211 Hei/Dic)
x1
x1
x1
PRE/F/4631
PRE/F/4608b
PRE/F/1688


1
2
PRE/F/3168a
x1
3
PRE/F/2009
x2
4
PRE/F/2009
x4
Matatiele
(Mat 111 Dic dub)
PRE/F/9175
x1
Holotype
5
PRE/F/9174
x2
6
PRE/F/9174
x1
7
PRE/F/9173
x2
8
PRE/F/9175
x2
9
PRE/F/9175
x4
10
PRE/F/9175
x4
11
PRE/F/2068
x2
12
PRE/F/9203
x2
13
PRE/F/2069
x2

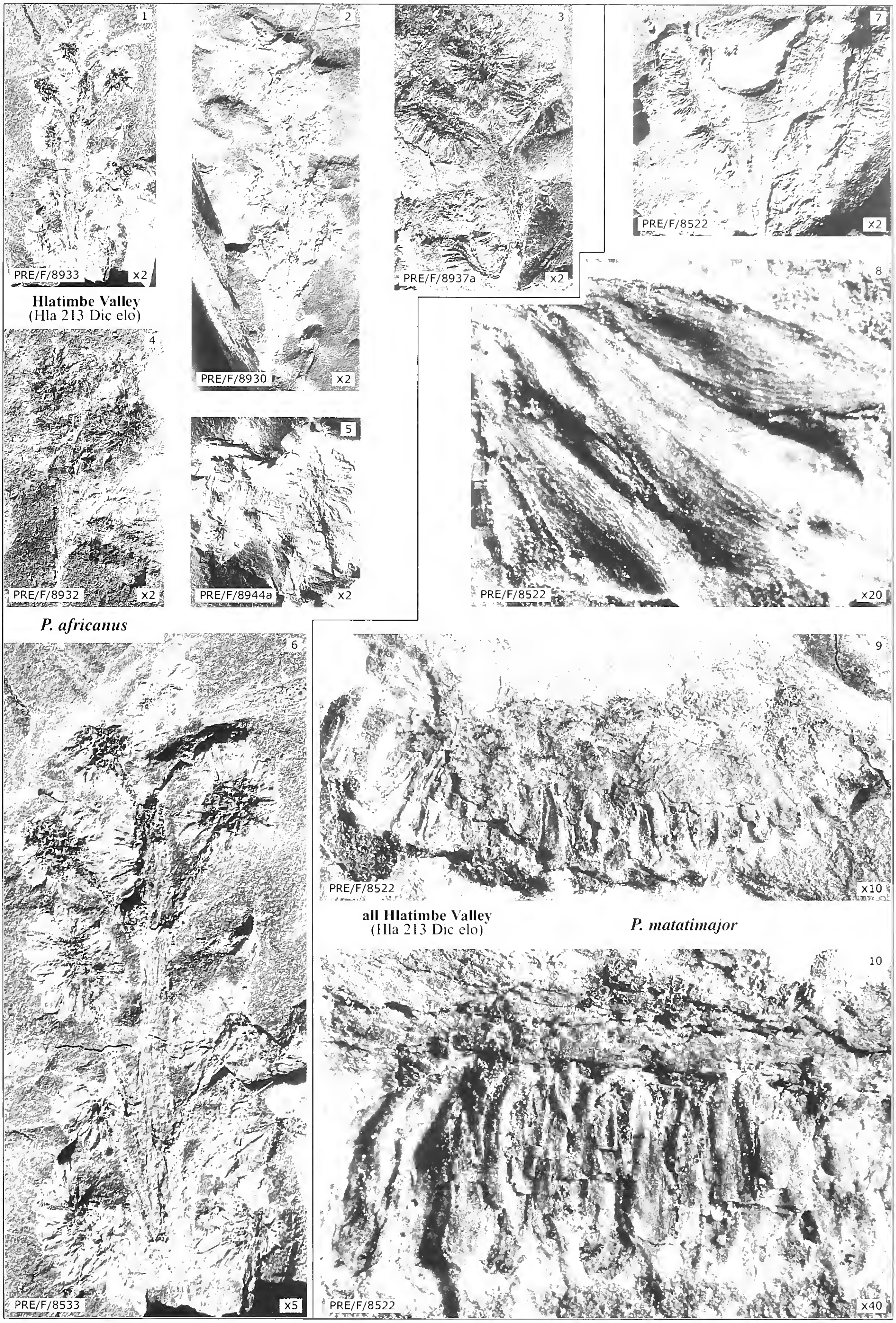


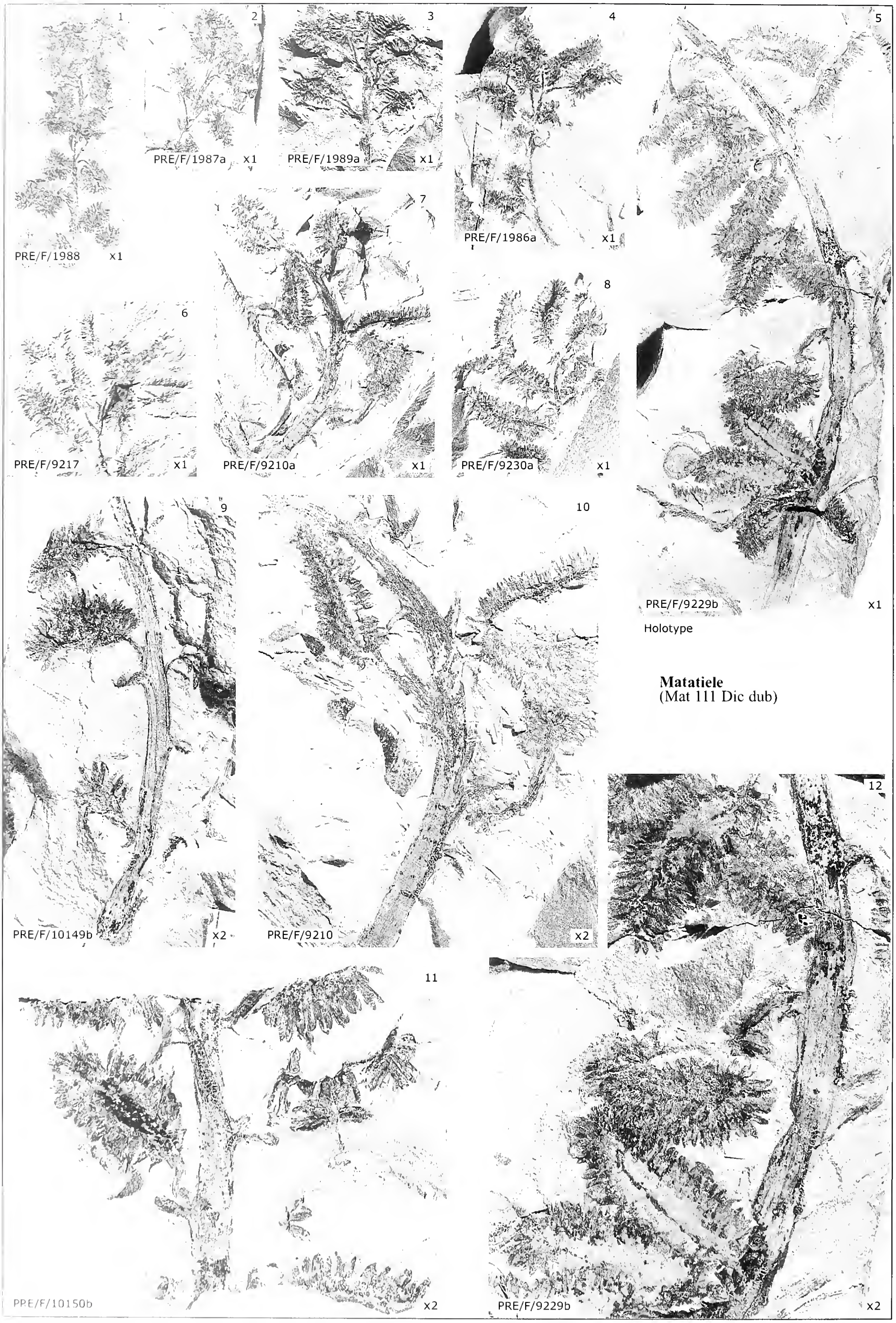
Little Switzerland
(Lit 111 Dic/Hei)


Konings Kroon
(Kon 222 Dic odo)
U. cupulata
1
BP/2/4122a
x1
Holotype
2
BP/2/4122a
x2
3
PRE/F/19999
x1
4
PRE/F/19999
x1
5
PRE/F/20339
x2
6
7
Morija
(Mor 111 Dic odo)
U. grandis
PRE/F/3397a
x2
PRE/F/3397a
Holotype
x1
8
PRE/F/3396
x2

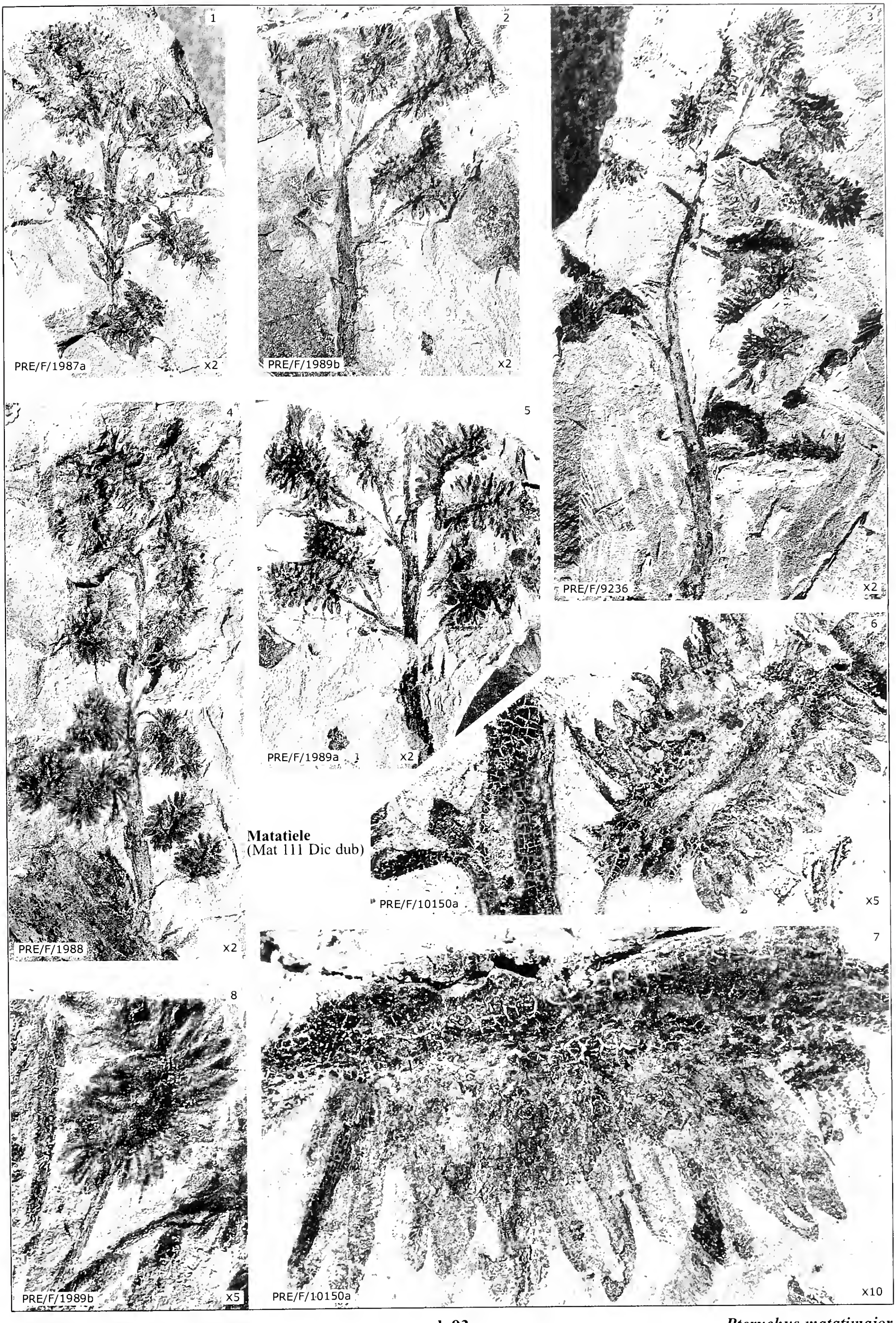


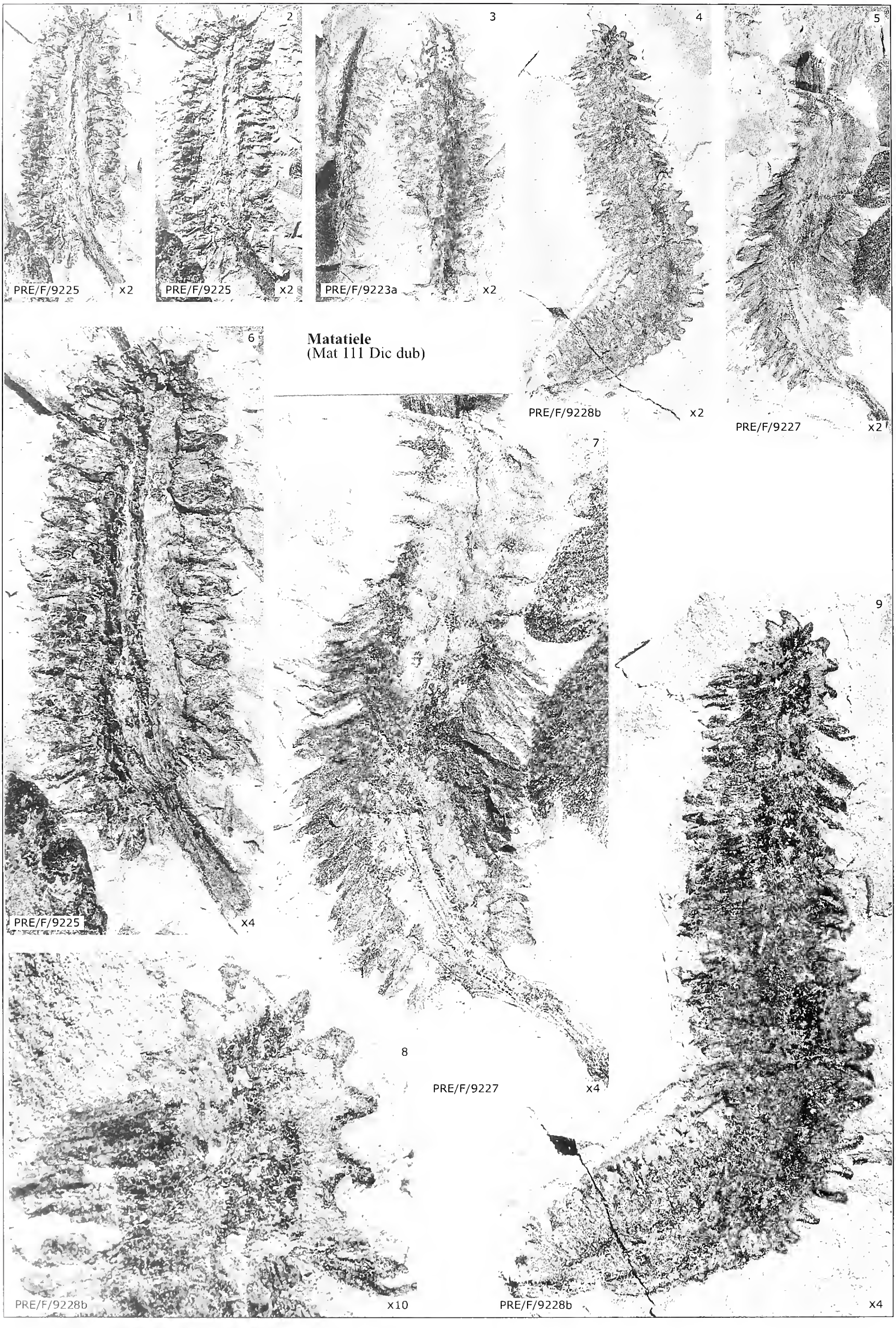
Pteruchus africanus **pl. 90** **UMKOMASIALES**


1
PRE/F/8933
x2
2
PRE/F/8930
x2
3
PRE/F/8937a
x2
7
PRE/F/8522
x2
Hlatimbe Valley
(Hla 213 Dic elo)
4
PRE/F/8932
x2
5
PRE/F/8944a
x2
8
PRE/F/8522
x20
P. africanus
6
PRE/F/8533
x5
9
PRE/F/8522
x10
all Hlatimbe Valley
(Hla 213 Dic elo)
P. matatimajor
10
PRE/F/8522
x40

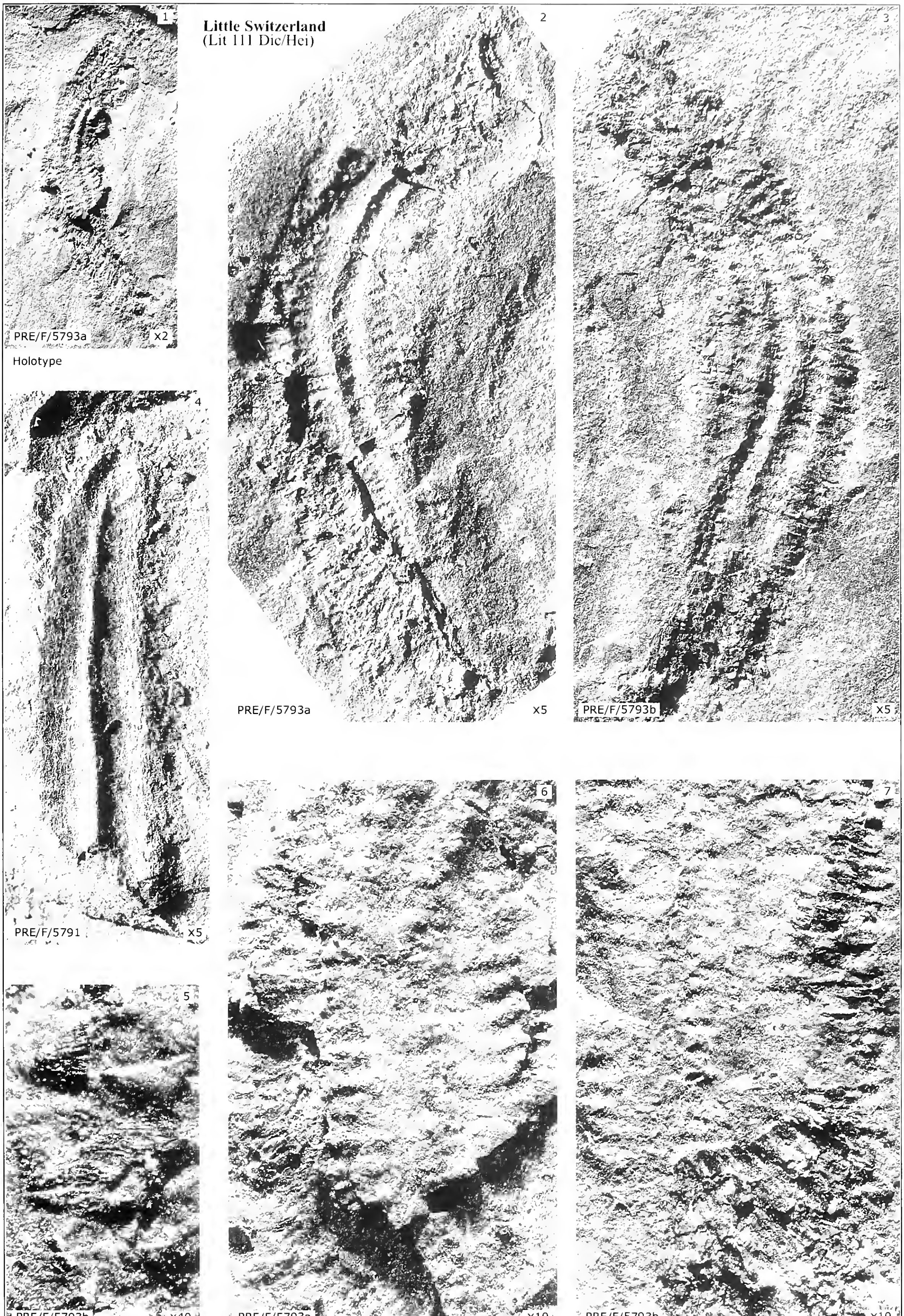


Matatiele
(Mat 111 Dic dub)


1
PRE/F/1987a
x2
2
PRE/F/1989b
x2
3
PRE/F/9236
x2
4
PRE/F/1988
x2
5
PRE/F/1989a
x2
6
PRE/F/10150a
x5
7
PRE/F/10150a
x10
8
PRE/F/1989b
x5
Matatiele
(Mat 111 Dic dub)



Pteruchus matatimajor **pl. 94** **UMKOMASIALES**



UMKOMASIALES pl. 95 *Pteruchus helvetigracilis*

GINKGOOPSIDA S.V.Meyen 1987
UMKOMASIALES S.V.Meyen 1984
UMKOMASIACEAE S.V.Meyen 1984

Fanerotheca Freng. 1944c

Type species
Fanerotheca extans Freng. 1944c.
Zanjòn, Potrerillos Fm., Cacheuta Basin, Argentina; U. Triassic.

Generic diagnosis emended
A ginkgoopsid strobilus of lax paniculate form with megasporophylls bearing 1–4 pairs of uni-ovulate cupules with strongly winged seeds.

Generic characters
Strobilus: simple, lax, paniculate, of medium size (*ca* 70 mm long); axis generally robust, erect, gradually tapering; megasporophylls several, apparently irregularly helical.
Megasporophyll: simple, pedunculate, spicate; bracteoles more or less prominent, variously scattered along axis and peduncles; ovuliferous cupules recurved, pedicellate, in 1–4 opposite to subopposite pairs.
Cupule: of medium size (4–8 mm deep), uni-ovulate, enclosing proximal half of mature seed, splitting into 4 lobes.
Seed: bilaterally symmetrical, strongly platyspermic and strongly winged; micropyle bifid, not curving to one side.

Etymology
Fanerotheca—not given by Frenguelli (1944c).

Global range: 5 spp., Gondwana, Tr. (CRN).
First & last: Molteno Fm.

Gondwana Triassic occurrence
SAm—Cacheuta Basin, 3 or 4 TCs (14 indivs).
SAf—Karoo Basin, 26 TCs (260 indivs).
Aus—Ipswich Basin, 1 TC (1 indiv.).

Molteno occurrence (see Tab. 56)
Frequency (F): 26 TCs (of 100 sampled in Molteno).
Diversity (D): 4 species.
Abundance (A): 260 indivs total; rare to very rare in top 6 TCs.

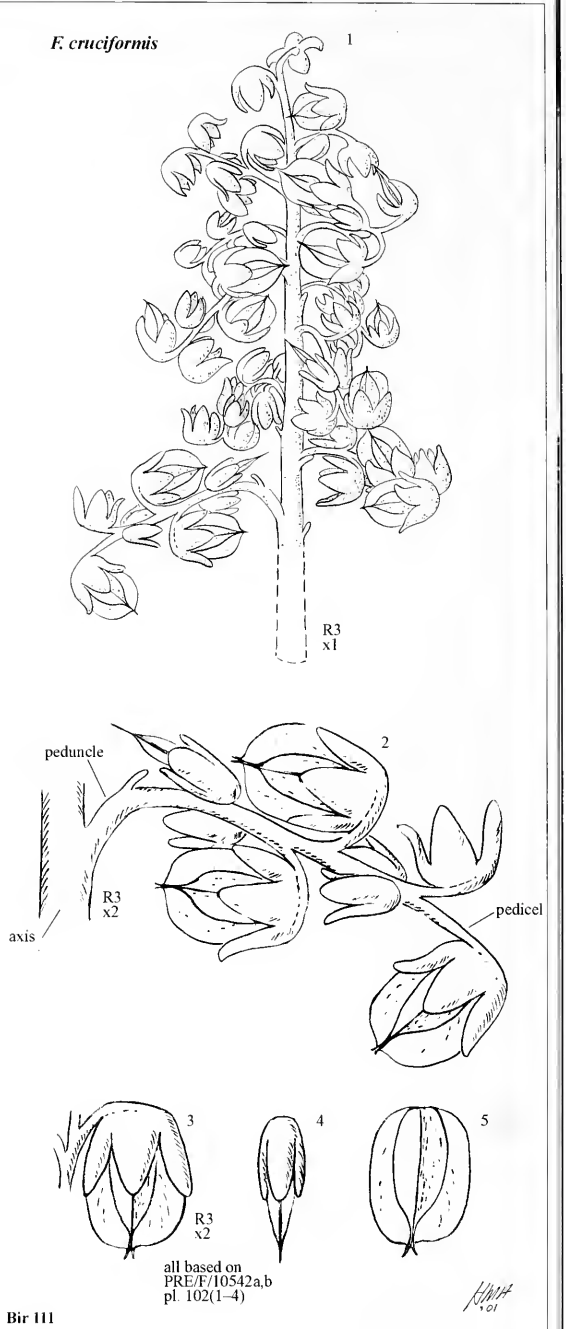
Kap 111 Dic/Ris:	40 indivs in	65 man-hrs cleaving	(7 per 1 man-day)	rare
Wal 111 Dic odo:	24 " "	50 " "	(4 " 1 ")	"
Bir 111 Hei/Sph:	60 " "	550 " "	(>1 " 1 ")	very rare
Lut 311 Hei elo:	7 " "	50 " "	(2 " 1 ")	" "
Umk 111 Dic 2spp:	30 " "	400 " "	(1 " 1 ")	" "
Aas 411 Dic/Sph:	47 " "	512 " "	(1 " 1 ")	" "

Affiliated organs
Male strobilus: unknown.
Foliage: *Dicroidium*—Grade 2 (Mut. occ.).

Classification & comparison
Suprageneric classification (Umkomasiaceae/Umkomasiales)
As *Fanerotheca* is closely allied to *Umkomasia*, we include it in the family Umkomasiaceae and order Umkomasiales in the class Ginkgoopsida.

Intergeneric comparison (Gondwana Triassic)
The lax strobilus of *Fanerotheca* is in many features like *Umkomasia*, but the cupules with strongly winged seeds (*Feruglioa*, Frenguelli 1944c) sets them generically apart.

Townrow (1960) reclassified *Fanerotheca* as *Antevsia*, having incorrectly interpreted the cupule lobes as sporangial sacs. In And. & And. [1983, pl. 23(3, 4)], we followed Townrow and used the genus *Antevsia* for strobili from Bir 111 that are here placed in *Fanerotheca* (*F. papilioformis*). The clear attachment of the winged seeds leaves no doubt that this is a female strobilus and that it is unrelated to *Antevsia*, a pollen-bearing organ.



Reconstructions
Strobilus
The reconstruction (tf. 1) is based on the type specimen of *F. cruciformis*, PRE/F/10542a,b, pl. 102(1–4), an almost complete strobilus requiring little restoring. The axis may extend basally.

Megasporophyll
A typical megasporophyll has been drawn for each of the four species (p. 275, tfs 1, 5, 9, 13).

Cupule & seed
Cupules of *F. cruciformis* with attached winged seeds are shown in lateral and end view (p. 272, tfs 3, 4). A similar reconstruction has been made for *F. papilioformis* and *F. waldeckiformis*, but not *F. elandiformis* for which information on cupules is lacking. All species and localities indicate one seed per cupule, similar to the case in *Umkomasia*.

Gondwana Triassic occurrence (elaborated)

Fanerotheca was first described from Argentina (Frenguelli 1944c), where it is fairly common in the Cacheuta area (Tab. 55)—14 specimens from three or four localities. *Fanerotheca exstans* Freng., while lacking some of our diagnostic features, is retained as the valid type species for the genus. *F. dichotoma* (Tab. 55) is here regarded as indeterminate. Australia has yielded only a single fragmentary specimen, from Denmark Hill (Walkom 1915), which is the earliest record of *Fanerotheca* from Gondwana.

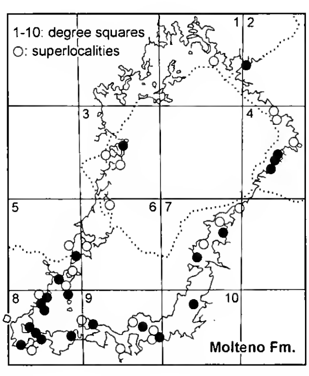
Molteno occurrence (elaborated)

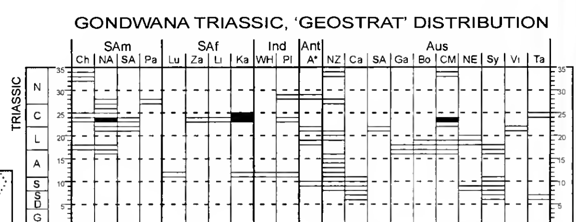
Fanerotheca, occurring at 27 TCs (Tab. 56), is the most frequent of all ovulate genera in the Molteno. The next most frequent is *Umkomasia*, which occurs at 22 TCs (Tab. 52). However, the reverse holds when considering abundance, *Umkomasia* with 503 individuals being more abundant than *Fanerotheca* with 247 individuals.

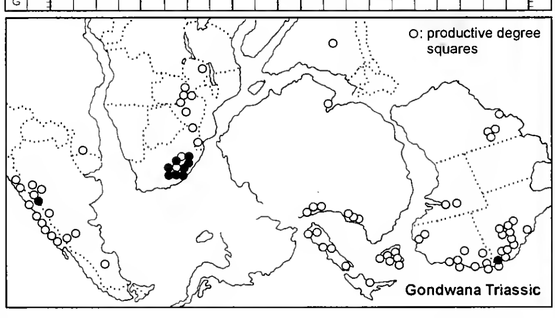
Tab. 55

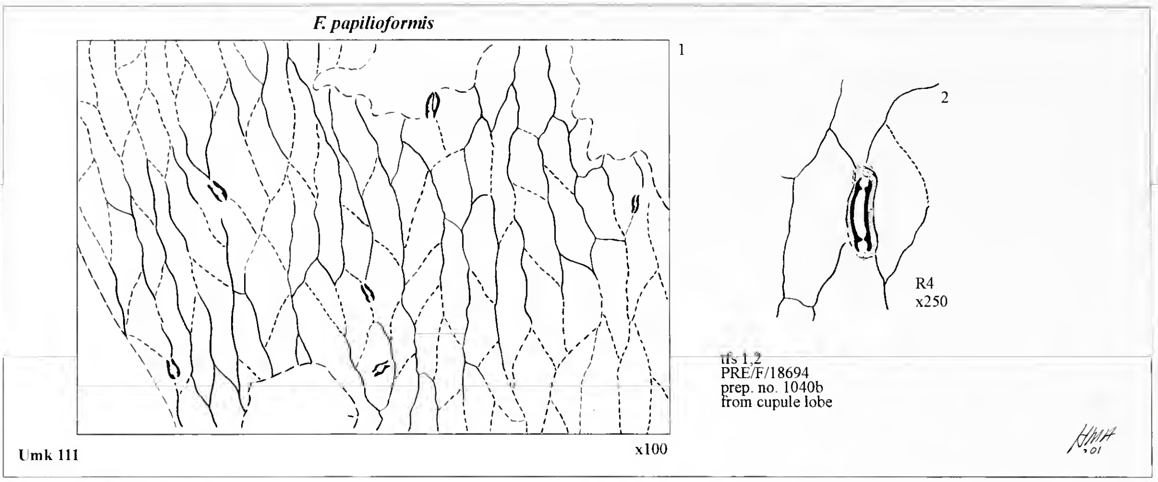
***FANEROTHECA* HYPODIGM, Gondwana Triassic occurrence**

AUTHOR		SUBREGION (°sq.)		FORMATION		LOCALITY	NAME (original)	Indivs	ILLUSTRATION	Species: Molteno: *F. papilioformis*	*F. waldeckiformis*	*F. cruciformis*	*F. elandiformis*	*F. exstans*	*F. spp. indet*	Intactness: Intact strobili	Fragmentary	Isolated megasp.
SOUTH AMERICA																		
1944c	Frenguelli	Cacheuta	NA4	24	Potrerillos	Zanjòn	*Fanerotheca exstans*	4	pl 1(1,2), 2(1), 3(1,2)	-	-	-	-	4	-	2	2	-
"	"	"	"	"	"	YPF Old Admin. Bld.	" "	3	pl 3(3), 4(1,2)	-	-	-	-	3	-	-	-	3
"	"	"	"	"	"	?Locality	" *dichotoma*	1	pl 2(2,3)	-	-	-	-	-	1	-	1	-
1946	"	"	"	"	"	-	*Stachyopitys anthoides*	1	pl 4(3)	-	-	-	-	1	-	1	-	-
1960	Townrow (specimen repeated from Frenguelli 1944c, pl 1(1))						*Antevsia exstans*	*	-	-	-	-	-	*	-	*	-	-
1967	Jain & Del.	"	"	"	"	Minas de Petroleo	*Fanerotheca exstans*	3	pl 90(11-13)	-	-	-	-	3	-	-	1	2
"	"	"	"	"	"	" "	incertae sedis	2	pl 90(9,10)	-	-	-	-	2	-	-	2	-
SOUTH AFRICA																		
1927	Du Toit	Elliot	Ka9	24	Molteno	Cala (2mls West)	*Sagenopteris sp.*	1	pl 29(3)	-	-	-	-	-	1	-	-	1
1960	Townrow	Underberg	Ka4	24	"	Upper Umkomaas	*Antevsia exstans*	1	tf 7(E,F), pl 58(6)	-	-	-	-	-	1	-	-	1
1979-1999 And. & And. Molteno literature not included in this table																		
AUSTRALIA																		
1915	Walkom	Ipswich/Esk	CM5	24	Blackstone Stage	Denmark Hill	*Equitsetites sp.*	1	pl 3(3,4)	-	-	-	-	-	1	-	1	-









Evidence for affiliation of organs

Foliage

There is no clear pattern of mutual occurrence for *Fanerotheca* and any foliage affiliate.

Fanerotheca is particularly common at Bir 111 and Aas 411, where it seems to have a link with the abundant *Sphenobaiera* (Tab. 50). But *Sphenobaiera* has now been securely affiliated with *Hamshawvia* and the attached immature fertile organ is definitely not *Fanerotheca*. Furthermore, at Kap 111 where *Fanerotheca* is also common, there are only 20 specimens of *Sphenobaiera* (under 1%).

At Bir 111 and Wal 111, although the frequency of *Dicroidium* is 1% and 92% respectively, no *Umkomasia* has been found (Tab. 56). This has led to our suggestion that *Fanerotheca* may be linked to *Dicroidium*, which is supported by: (1) the similarity in strobili and cupule structure of *Fanerotheca* and *Umkomasia*, and (2) *Fanerotheca* occurring in 13 TCs with *Dicroidium* but no *Umkomasia* (Tab. 52). However, at these 13 TCs there is no clear correlation with any particular *Dicroidium* species or group of species.

Male strobilus

The male affiliate is unknown, but it could possibly be a species of *Pteruchus* or *Stachyopitys* (see Tabs 50 and 54 for the distribution of these two genera along with that of *Fanerotheca*).

Seed

The seed now known attached to *Fanerotheca* (Grade 5 affiliation) was originally described by Frenguelli (1944c) as *Feruglioa samaroides*. From the same locality, Frenguelli also described *Fanerotheca extans*, but he did not record any of the seeds as being attached.

Intactness & preservation

In situ seeds

F. cruciformis—In the most complete strobilus from Bir 111, PRE/F/10542a,b, pl. 102(1–4), four seeds, one per cupule, remain attached. These appear to be mature and are *ca* twice as long as the cupule.

F. papilioformis—At Bir 111, one strobilus shows a single attached seed which is twice the length of the cupule lobes [BP/2/5199b, pl. 97(2, 3)]. Another shows several seeds attached, one to a cupule [BP/2/11854, pl. 96(3, 12)]. Further specimens show attached seeds but these are not illustrated here: Bir 111, BP/2/5201a, BP/2/5007; Umk 111, PRE/F/1694.

F. waldeckiformis—At Wal 111 all specimens have lost their seeds, while at Mat 111 a single strobilus, PRE/F/2010, pl. 101(8), shows seeds still attached to the cupules.

Germinating seeds

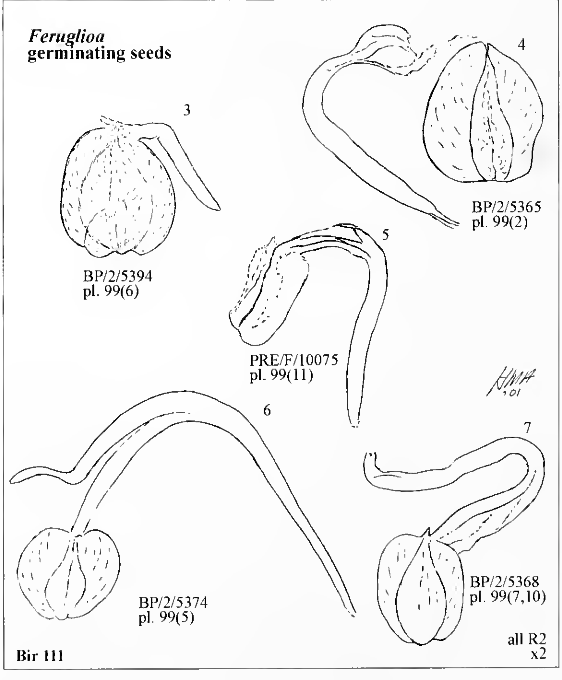
At Bir 111, the winged seeds, *Feruglioa*, occur massed on certain bedding planes. Some show evidence of having germinated by the presence of a distinct radicle emerging from the micropyle end of the seed. This can be seen in various specimens, some also with their first leaves (tfs 3–7 adjacent; pl. 99). Krassilov (1987, pl. 4) illustrates very similar germinating seeds and seedlings, with clear elongate leaves, from the Jurassic of Ust-Balej (USSR).

Cuticles

Potential sample: Lit 111, 3 indivs; Umk 111, 16 indivs.
Macerated (this work): Umk 111, 2 indivs from cupule lobe.
Preservation grade: Grade 3, some features including stomata visible.
Diagnostic characters: cells isodiametric to narrowly pentagonal to linear-oblong, walls gently curved, nonpapillate; stomata (?)amphistomatic, orientation longitudo-random, subsidiary cells nonlappetate brachy-paracytic, guard cells narrowly elliptic.
Comment: the illustrated cuticle derives from the cupule lobe.
Significance:

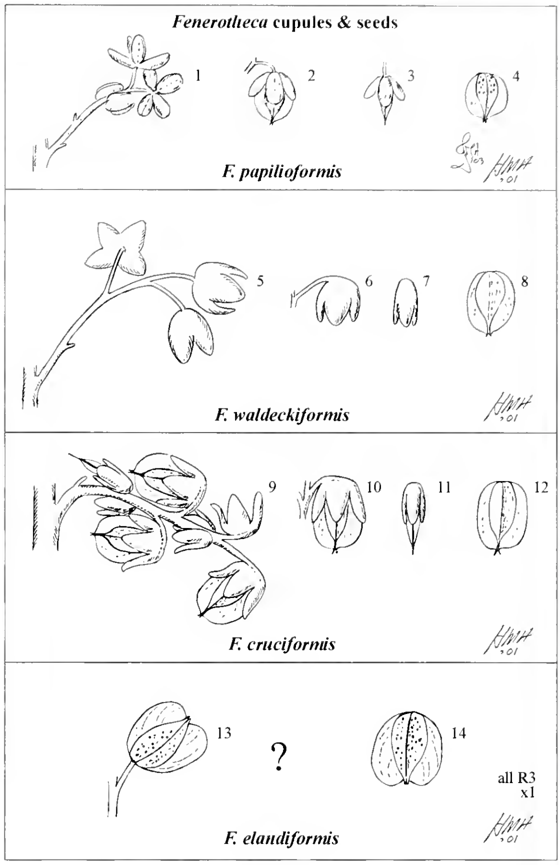
Classification—Though the macerated cuticle is thin and not too clearly preserved, it is sufficient to support the classification of *Fanerotheca* in the order Umkomasiales and class Ginkgoopsida.

Affiliations—In its subsidiary cells being nonlappetate and brachy-paracytic, *Fanerotheca* is clearly more like *Dicroidium* than any of the other typically ginkgoopsid foliage genera such as *Lepidopteris*, *Sphenobaiera*, *Ginkgoites* and *Dejerseya*. In being nonpapillate and having narrowly elliptic guard cells, it most nearly approaches the cuticle of *D. odontopteroides* forma *odontopteroides* (And. & And. 1983, p. 199). However, it does not show the cutinised subsidiary cells or trichome bases of the latter taxon.



assemblages (taphocoenosis)	Genera: *Dicroidium*	♀ *Umkomasia*	♂ *Pteruchus*	♀ *Fanerotheca*	Species: *F. papilioformis*	*F. waldeckiformis*	*F. cruciformis*	*F. elandiformis*	*F. spp. indet*	Intactness: Intact strobili	Partial "	Isolated heads	Dispersed seeds
Ken 111 Dic cra	**99**	-	-	-	-	-	-	-	-	-	-	-	-
Nav 111 Dic odo	**98**	-	-	1	-	1	-	-	-	1	-	-	-
Cal 111 Dic/Sph	**50**	-	-	-	-	-	-	-	-	-	-	-	-
Bir 211 Sph 2spp	**4**	-	-	1	-	-	-	-	1	-	-	1	-
311 Hei/Sph	**14**	2	1	2	2	-	-	-	-	1	-	1	✓
111 Sph 2spp	**1**	-	-	60	52	-	8	-	-	22	24	14	✓✓✓
Gre 121 Hei elo	3	-	-	-	-	-	-	-	-	-	-	-	-
111 Equ sp	**2**	-	-	3	3	-	-	-	-	-	3	-	✓
Boe 111 Lep sto	5	-	-	1	1	-	-	-	-	-	1	-	-
" Dic/Hei	**57**	-	-	-	-	-	-	-	-	-	-	-	-
112 Dic cor	**99**	8	10	-	-	-	-	-	-	-	-	-	-
Cyp 111 Dic cra	**75**	2	-	1	-	-	-	-	1	-	-	1	-
Mol 111 Sph pon	12	-	-	1	1	-	-	-	-	1	-	-	-
Kan 112 Hei elo	**1**	-	-	-	-	-	-	-	-	-	-	-	-
Tel 111 "	**6**	-	1	2	2	-	-	-	-	1	1	-	✓
Kom 111 Sph/Dic	**39**	-	-	2	2	-	-	-	-	1	1	-	✓
Vin 111 Dic odo	**70**	-	-	-	-	-	-	-	-	-	-	-	-
Ela 111 "	**87**	1	3	1	-	1	-	-	-	1	-	-	✓
Kra 311 "	**99**	-	-	-	-	-	-	-	-	-	-	-	-
221 Beetles	**50**	-	-	-	-	-	-	-	-	-	-	-	-
111 Dic odo	**90**	14	30	-	-	-	-	-	-	-	-	-	-
Lut 111 Hei/Dic	**40**	-	-	-	-	-	-	-	-	-	-	-	-
411 "	**50**	-	-	-	-	-	-	-	-	-	-	-	-
311 Hei elo	58	-	-	7	7	-	-	-	-	-	1	6	✓✓✓
221 Equ sp	**1**	-	-	-	-	-	-	-	-	-	-	-	-
Tin 121 Sph 2spp	**1**	-	-	1	1	-	-	-	-	1	-	-	✓✓
Wal 111 Dic odo	**92**	-	-	24	-	24	-	-	-	10	8	6	✓✓✓
Kon 223 "	**80**	-	-	-	-	-	-	-	-	-	-	-	-
222 "	**87**	22	13	1	1	-	-	-	-	1	-	-	-
211 Hei elo	5	-	-	-	-	-	-	-	-	-	-	-	-
111 Dic odo	**78**	-	1	-	-	-	-	-	-	-	-	-	-
" Hei elo	3	-	-	-	-	-	-	-	-	-	-	-	-
Pen 321 Dic/Ris	**51**	-	-	-	-	-	-	-	-	-	-	-	-
211 Dic/Equ	**50**	-	-	-	-	-	-	-	-	-	-	-	-
221 "	**40**	-	-	-	-	-	-	-	-	-	-	-	-
511 Equ sp	**2**	-	-	-	-	-	-	-	-	-	-	-	-
421 Dic odo	**89**	-	-	-	-	-	-	-	-	-	-	-	-
431 Dic/Equ	**40**	-	-	-	-	-	-	-	-	-	-	-	-
311 Hei elo	**25**	3	4	-	-	-	-	-	-	-	-	-	-
411 "	13	-	-	-	-	-	-	-	-	-	-	-	-
Kle 111 Hei/Dic	**45**	-	-	1	-	1	-	-	-	1	-	-	✓✓
Kap 111 Dic/Ris	**50**	2	11	40	40	-	-	-	-	3	26	11	✓✓✓
Ela 112 Equ sp	**1**	-	-	-	-	-	-	-	-	-	-	-	-
" Dic/Hei	**60**	-	-	2	-	-	-	2	-	-	2	-	✓✓
Nuw 111 Dic zub	**70**	11	15	-	-	-	-	-	-	-	-	-	-
211 Dic 2spp	**98**	-	-	-	-	-	-	-	-	-	-	-	-
Win 111 Hei elo	**10**	-	-	-	-	-	-	-	-	-	-	-	-
Mor 111 Dic zub	**99**	-	-	-	-	-	-	-	-	-	-	-	-
" Dic odo	**98**	3	1	-	-	-	-	-	-	-	-	-	-
Qua 111 "	**40**	1	-	-	-	-	-	-	-	-	-	-	-
Mak 111 "	**90**	-	-	-	-	-	-	-	-	-	-	-	-
Maz 111 Dic cra	**74**	-	6	6	-	-	6	-	-	1	2	3	✓✓✓
211 Hei/Dic	**64**	46	27	5	5	-	-	-	-	1		4	✓✓✓
Moo 111 Dic zub	**99**	-	-	-	-	-	-	-	-	-	-	-	-
Hla 111 Equ sp	**1**	-	-	-	-	-	-	-	-	-	-	-	-
211 Dic 3spp	**85**	3	2	3	-	-	-	-	3	-	1	2	-
212 "	**91**	4	4	-	-	-	-	-	-	-	-	-	-
213 Dic elo	**89**	32	22	5	-	-	-	-	5	-	2	3	✓
Umk 111 Dic 2spp	**69**	197	138	16	16	-	-	-	-	4	9	3	✓✓✓
Cha 111 Dic odo	**100**	-	-	-	-	-	-	-	-	-	-	-	-
211 Dic dub	**80**	-	-	-	-	-	-	-	-	-	-	-	-
Inj 111 Dic odo	**100**	-	-	-	-	-	-	-	-	-	-	-	-
211 Dic dub	**90**	-	-	-	-	-	-	-	-	-	-	-	-
San 111 Dic cra	**90**	4	5	5	5	-	-	-	-	1	-	4	✓
Mng 111 Dic 2spp	**93**	-	-	-	-	-	-	-	-	-	-	-	-
Qac 111 Hei/Dic	**50**	-	-	-	-	-	-	-	-	-	-	-	-
Mat 111 Dic dub	**89**	75	50	6	-	6	-	-	-	2	3	1	✓
Gol 111 "	**99**	1	1	-	-	-	-	-	-	-	-	-	-
Lit 111 Dic/Hei	**50**	51	36	3	3	-	-	-	-	1	1	1	-
Aas 111 Hei elo	7	-	-	-	-	-	-	-	-	-	-	-	-
311 "	15	-	-	-	-	-	-	-	-	-	-	-	-
411 Dic/Sph	**60**	7	3	47	47	-	-	-	-	11	26	10	✓✓✓
511 Dic elo	**50**	-	-	-	-	-	-	-	-	-	-	-	-
Ask 111 Equ sp	**21**	14	15	-	-	-	-	-	-	-	-	-	-
Bam 111 Dic dub	**98**	-	-	-	-	-	-	-	-	-	-	-	-
Total TCs	75	22	23	27	16	5	2	1	4	19	16	16	19
Total indivs	%	503	425	247	188	33	14	2	10	65	111	71	

Tab. 56. ***Fanerotheca*****, Molteno occurrence**



Adaptive radiation (Molteno diversity)

Although *Fanerotheca* occurs frequently and commonly in the Molteno—247 individuals (65 of which are intact) from 27 TCs—it is markedly lacking in evident diversity. Only four species can be differentiated. The diagnostic characters lie essentially in the robustness of the strobilus, the number of cupule pairs, and in the nature of the cupules and length of their pedicels.

The four species, based on very variably sized palaeodemes, are all from floodplain habitats—either *Dicroidium* or *Sphenobaiera* woodland. This is in marked contrast to the *Umkomasia* species which are mainly from *Dicroidium* forest habitats.

F. papilioformis—Bir 111 Sph 2 spp (Birds River), 52 indivs
Sphenobaiera closed woodland (floodplain lake); Cycle 5 (Tsomo Member)
F. waldeckiformis—Wal 111 Dic odo (Waldeck), 24 indivs
Sphenobaiera closed woodland (floodplain lake); Cycle 2 or 3
F. cruciformis—Bir 111 Sph 2 spp (Birds River), 8 indivs
Sphenobaiera closed woodland (floodplain lake); Cycle 5 (Tsomo Member)
F. elandiformis—Ela 112 Dic/Hei (Elandspruit), 2 indivs
Dicroidium open woodland (floodplain); Cycle 2a (Indwe Member)

Fanerotheca papilioformis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/10544a,b; pl. 96(1, 13).
Assemblage (TC): Bir 111 Sph 2spp, Birds River.
Preservation: complete specimen, part and counterpart; impression in thinly laminated, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 52 indivs (21 intact, 23 partial, 8 isolated), pls 96–99.

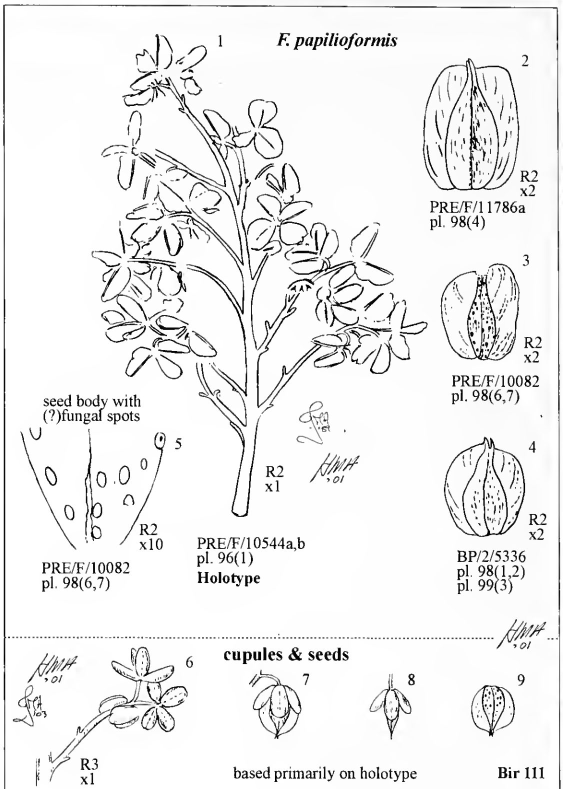
Sister palaeodemes—15 (best 2 listed)
Aas 411 Dic/Sph: 47 indivs (11 intact, 26 partial, 10 isolated).
Kap 111 Dic/Ris: 40 indivs (3 intact, 26 partial, 11 isolated).

Specific diagnosis
A *Fanerotheca* species with gracile strobili bearing megasporophylls with 1 or 2 pairs of cupules on short pedicels.

Specific characters
Megasporophyll: gracile; cupules in 1 or 2 pairs, opposite and decussate; pedicels short (1–3 mm).
Cupule: gracile, 2- to 4-lobed, with lobes deeply divided to pedicel attachment and folding tightly along midline.
Ovule/seed: relatively small (7.5–11 mm long), body occasionally covered with characteristic oval spots.

Etymology
papilioformis—*papilio* (Lat.), butterfly, with reference to the butterfly-shaped cupule lobes.

Comments & comparison
This is the most common and widespread (17 TCs) of the Molteno *Fanerotheca* species. It is very distinctive in that the lobes are always deeply divided to the point of attachment with the pedicel. The spots on the seed body may be secondary, i.e. of fungal origin.



Fanerotheca waldeckiformis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/9440a,b; pl. 100(2–4).
Assemblage (TC): Wal 111 Dic odo, Waldeck.
Preservation: almost complete specimen, part and counterpart; impression in thickly laminated, moderately baked, medium light grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 24 indivs (10 intact), pls 100(1–10), 101(1–7).

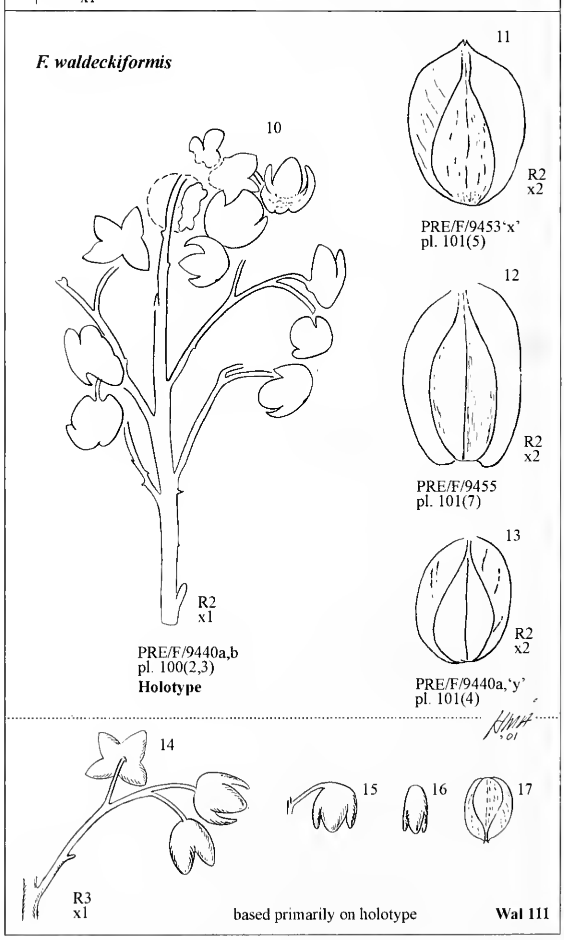
Sister palaeodemes—4 (best 1 listed)
Mat111 Dic dub: 6 indivs (2 intact, 3 partial, 1 isolated), pl. 101(8–13).

Specific diagnosis
A *Fanerotheca* species with fairly gracile strobili bearing megasporophylls with 1 or 2 pairs of cupules on long pedicels.

Specific characters
Megasporophyll: gracile; cupules in 1 or 2 pairs, clustered distally; pedicels long (4–8 mm).
Cupule: fairly robust, 4-lobed, with lobes divided *ca* midway to pedicel attachment.
Ovule/seed: intermediate in size (10–14 mm long), body without spots.

Etymology
waldeckiformis—with reference to the type locality.

Comments & comparison
This species is distinguished from *F. papilioformis* in the longer pedicels and shallower cupule lobing, and from *F. cruciformis* in the fewer cupule pairs.



Fanerotheca cruciformis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/10542a,b; pl. 102(1–4).
Assemblage (TC): Bir 111 Sph 2spp, Birds River.
Preservation: almost complete specimen, part and counterpart; impression in thinly laminated, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 8 indivs (1 intact, 1 partial, 6 isolated), pl. 102(1–7).

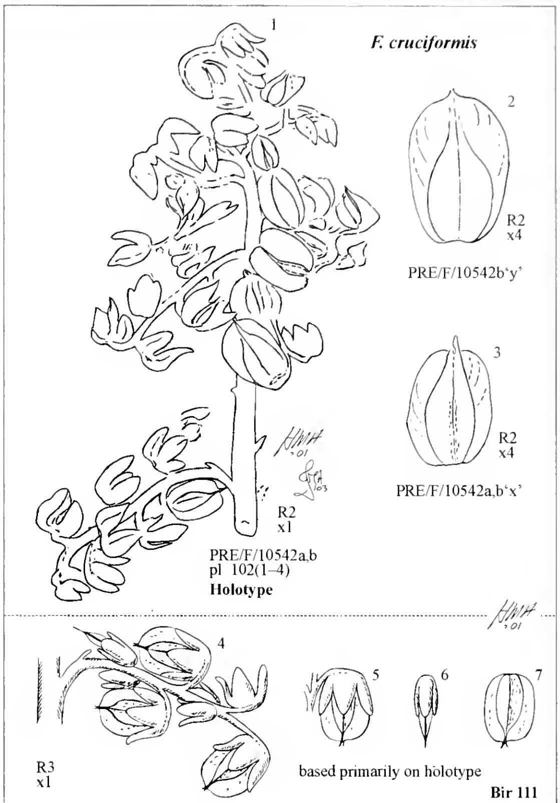
Sister palaeodemes—1 only (as listed)
Maz 111 Dic cra: 6 indivs (1 intact, 2 partial, 3 isolated).

Specific diagnosis
A *Fanerotheca* species with robust strobili bearing megasporophylls with 3 or 4 pairs of cupules on short pedicels.

Specific characters
Megasporophyll: robust; cupules in 3 or 4 pairs, subopposite and decussate; pedicels short (1–3 mm).
Cupule: fairly robust, 4-lobed, with lobes divided *ca* 3/4 to pedicel attachment.
Ovule/seed: intermediate in size (10–12 mm long), body without spots.

Etymology
cruciformis—with reference to the cross-shaped cupule lobes when open.

Comments & comparison
This second species of *Fanerotheca* from Bir 111, with only eight individuals (one intact), is by far the less common at this site. It is distinct from other species in being more robust and bearing three to four pairs of cupules.



Fanerotheca elandiformis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/13306a,b; pl. 103(6, 7).
Assemblage (TC): Ela 112 Dic/Hei, Elandspruit.
Preservation: incomplete specimen, part and counterpart; impression in thickly laminated, medium grey shale with poor cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 2 indivs (2 partial), pl. 103(1–9).

Sister palaeodemes—nil.

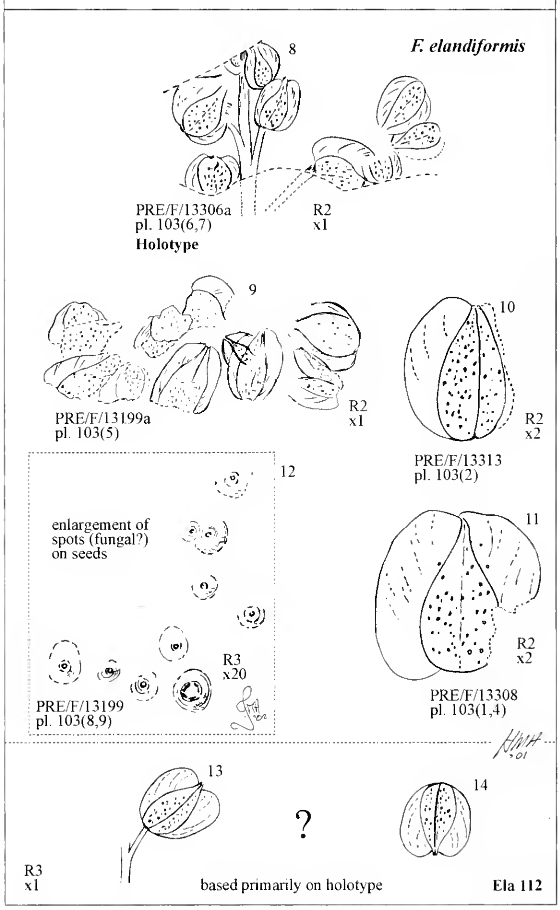
Specific diagnosis
A *Fanerotheca* species with strobili bearing megasporophylls with (?)2 or 3 pairs of naked seeds on fairly long pedicels.

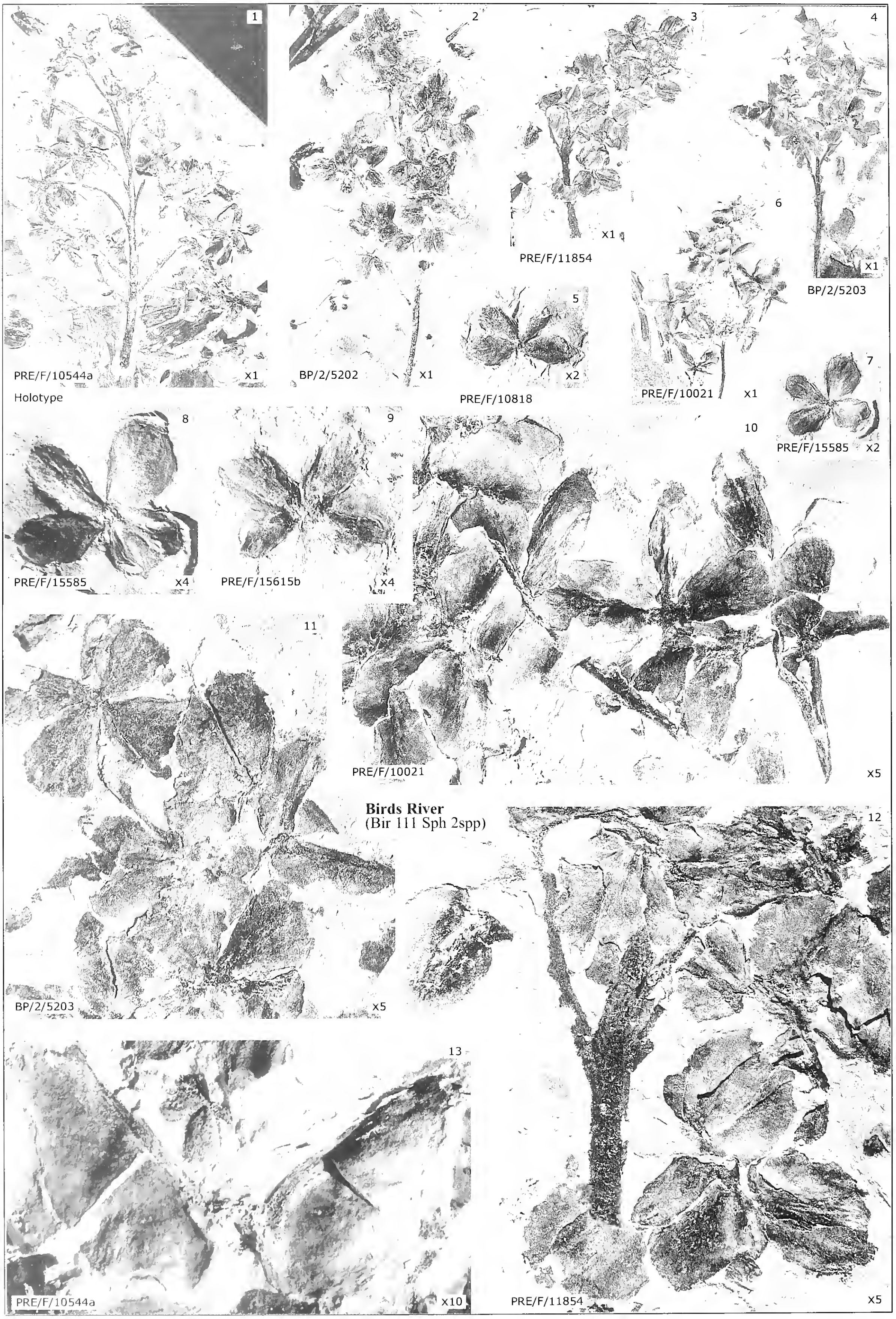
Specific characters
Megasporophyll: robust; naked seeds in (?)2 or 3 pairs; pedicels of intermediate length (3–5 mm).
Cupule: unknown.
Ovule/seed: relatively large (11–16 mm long), body invariably covered with characteristic protuberances.

Etymology
elandiformis—with reference to the type locality, Elandspruit.

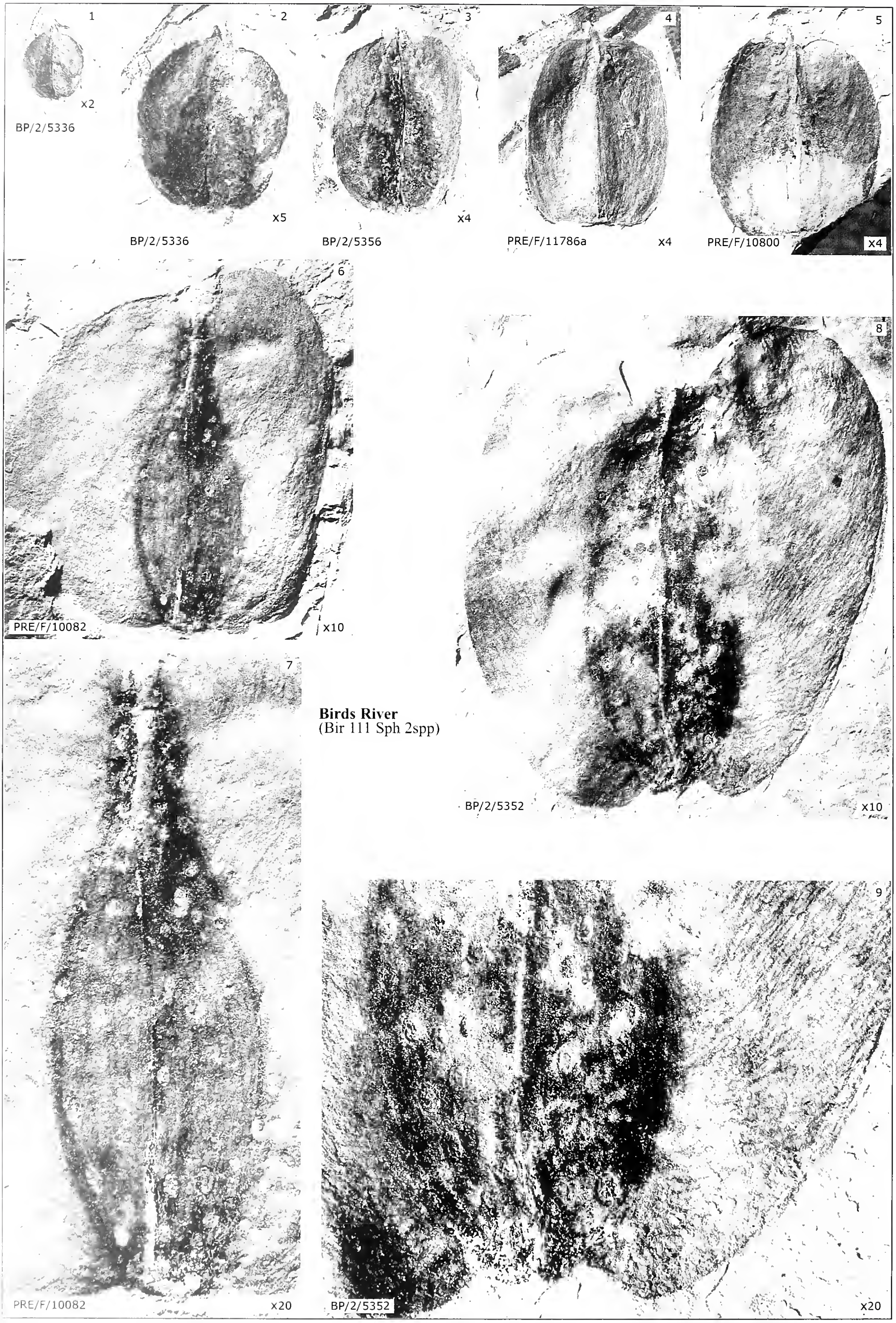
Comments & comparison
In view of the large seeds, this is clearly a distinct species. Also, the characteristic four-lobed cupules found in the other species are apparently absent—as witnessed in the holotype, the only partly intact specimen, which has naked seeds attached directly to the pedicels [pl. 103(7)].

The unique markings on the seeds are generally spherical, protruding, and differ from the more level, oval variety characterising *F. papilioformis*. It is possible that these markings are a secondary feature, such as fungal spots, in which case they are apparently host-specific. In *F. elandiformis* they occur consistently on all collected seeds, not the case in *F. papilioformis*.

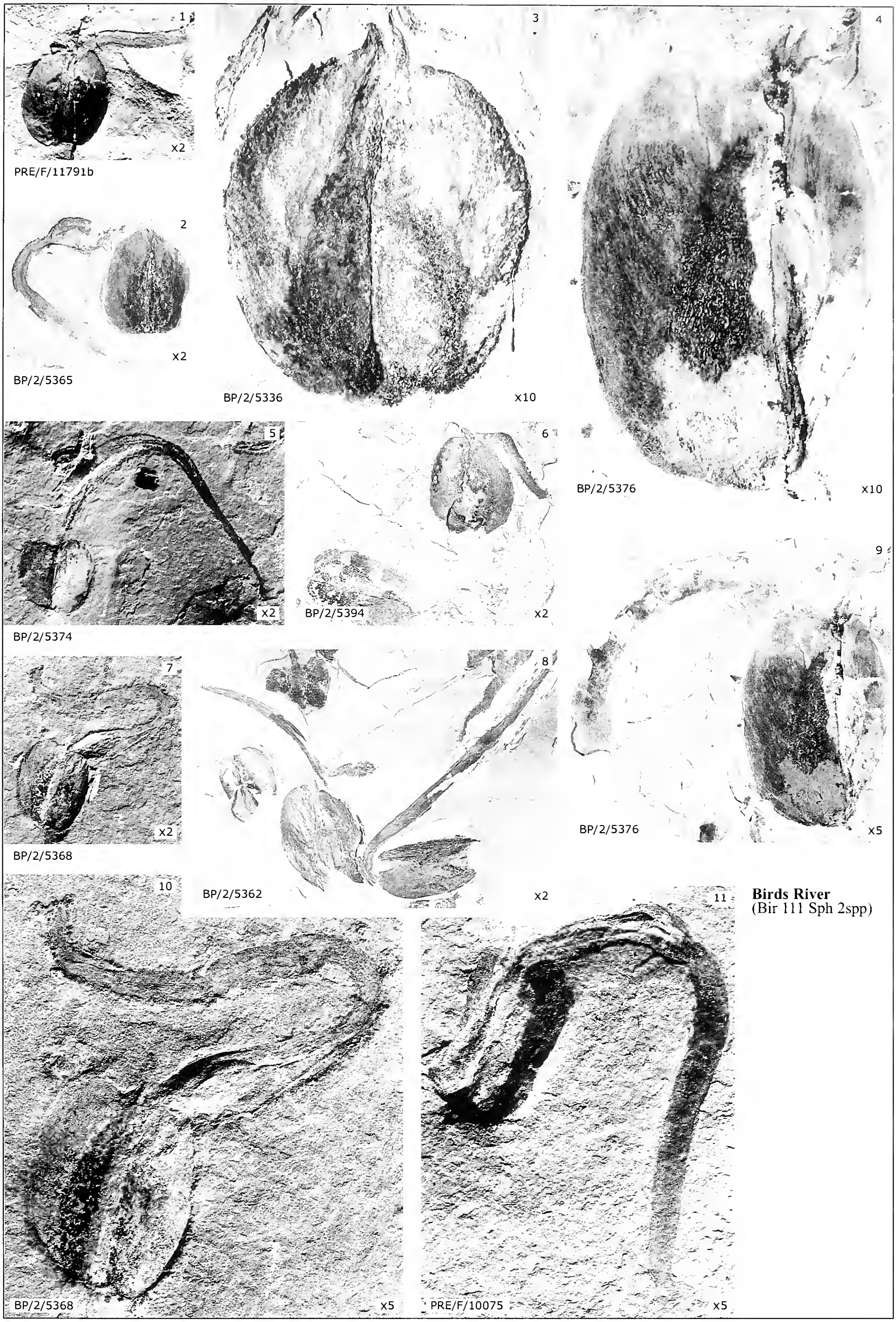



1
PRE/F/10544a x1
Holotype
2
BP/2/5202 x1
3
PRE/F/11854 x1
4
BP/2/5203 x1
5
PRE/F/10818 x2
6
PRE/F/10021 x1
7
PRE/F/15585 x2
8
PRE/F/15585 x4
9
PRE/F/15615b x4
10
PRE/F/10021 x5
11
BP/2/5203 x5
Birds River
(Bir 111 Sph 2spp)
12
PRE/F/11854 x5
13
PRE/F/10544a x10

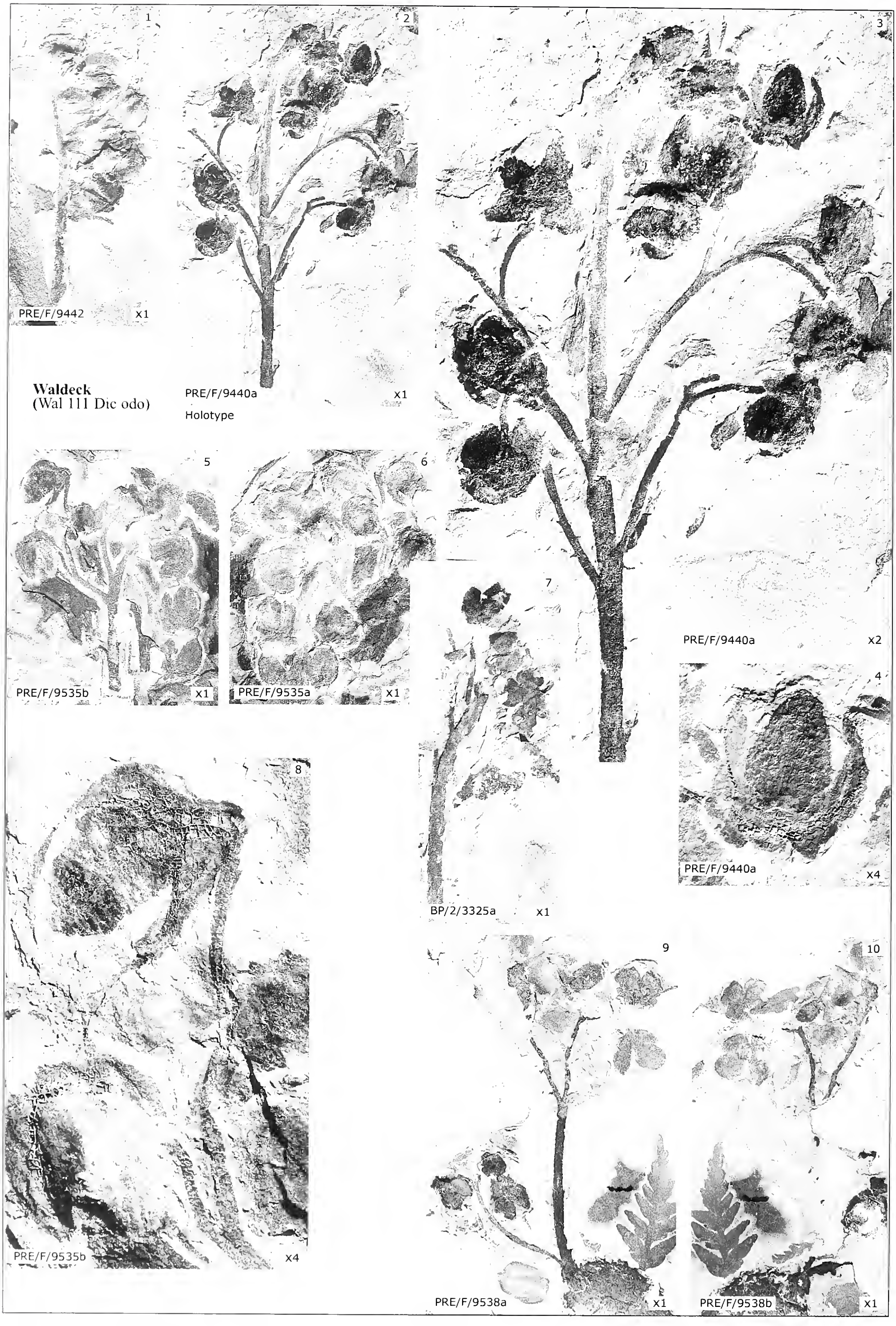

1
x1
2
all BP/2/5199b
3
x10
4
x40
x4
Birds River
(Bir 111 Sph 2spp)
5
x40
6
x20

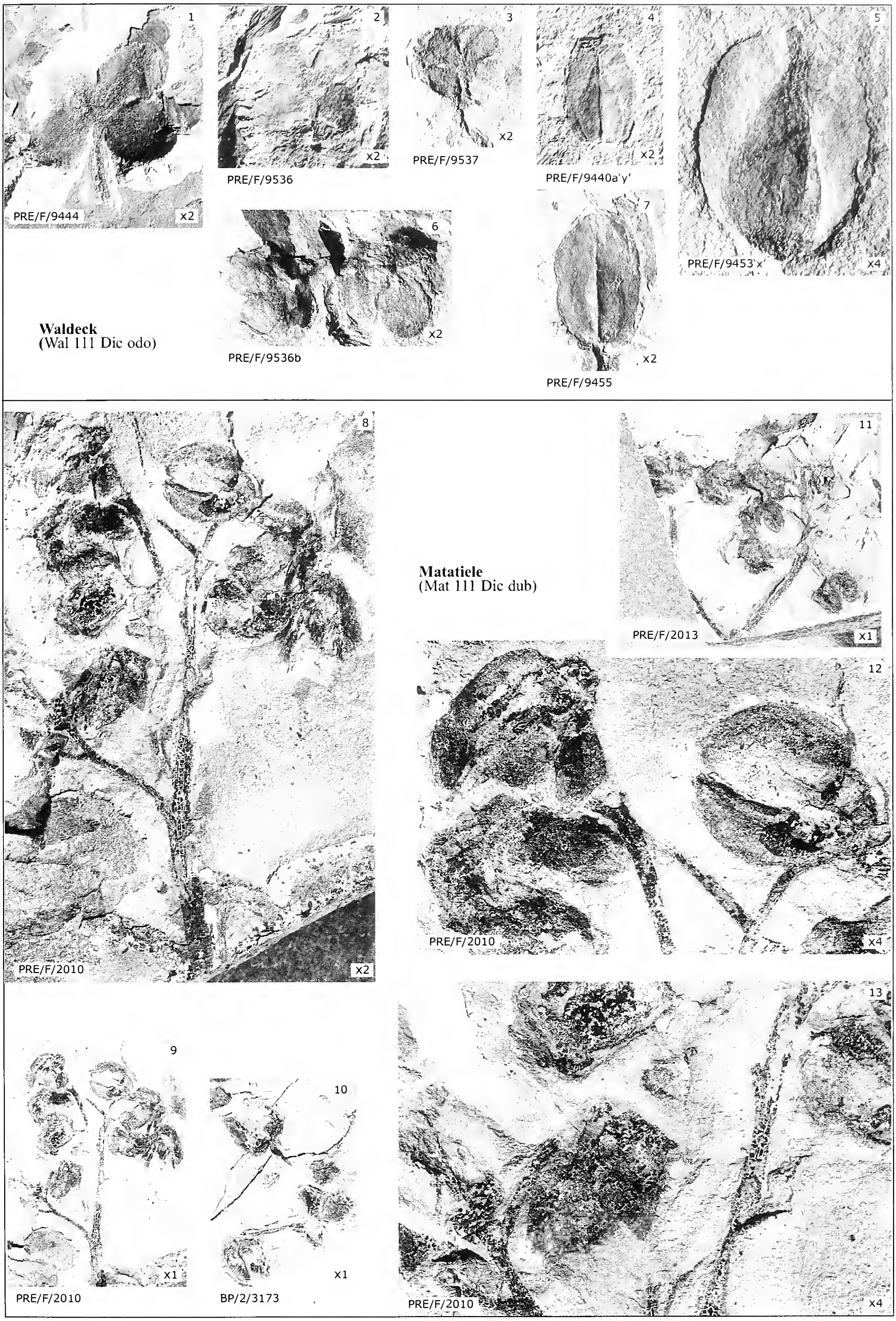


Birds River
(Bir 111 Sph 2spp)

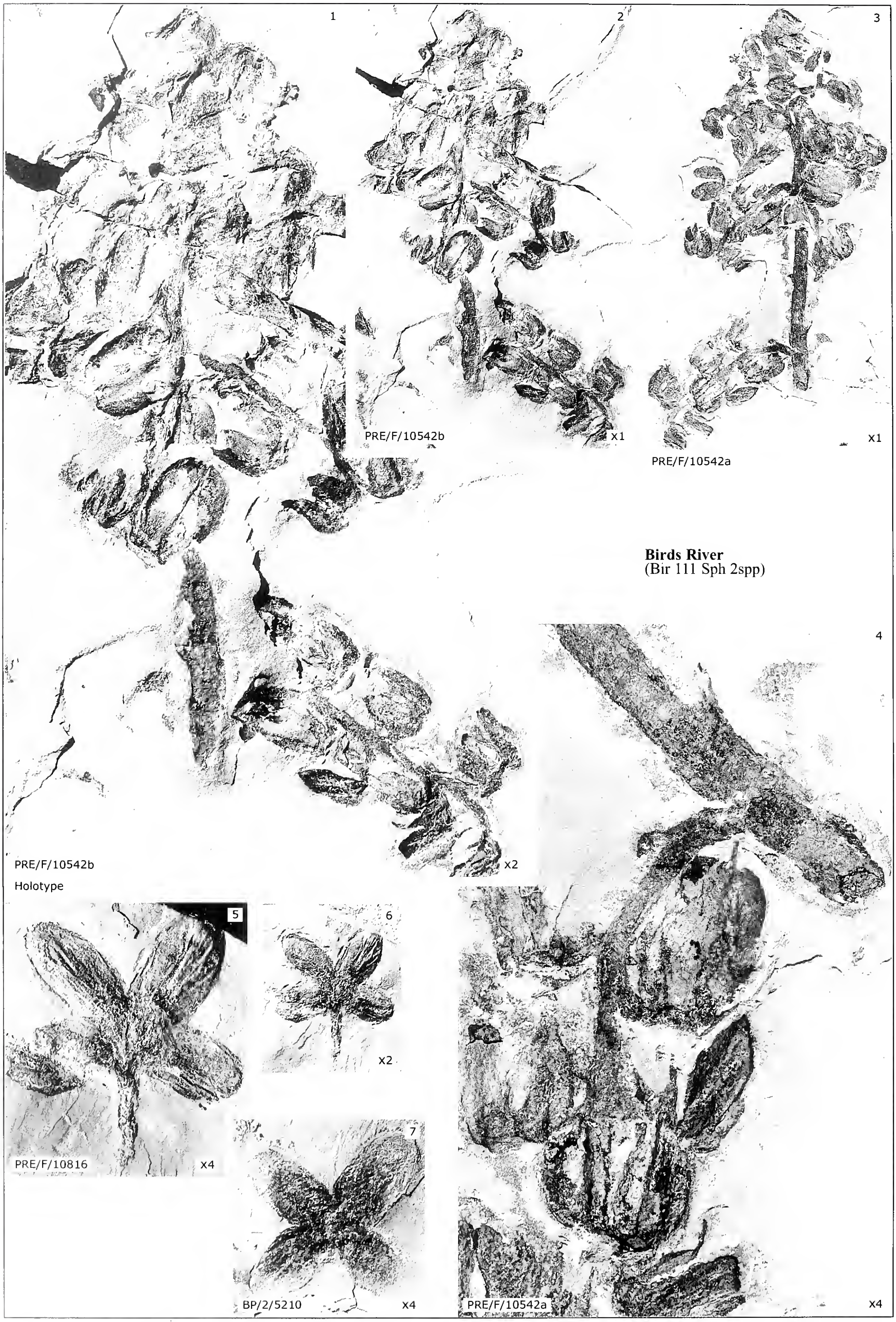


UMKOMASIALES pl. 99 *Fanerotheca papilioformis*

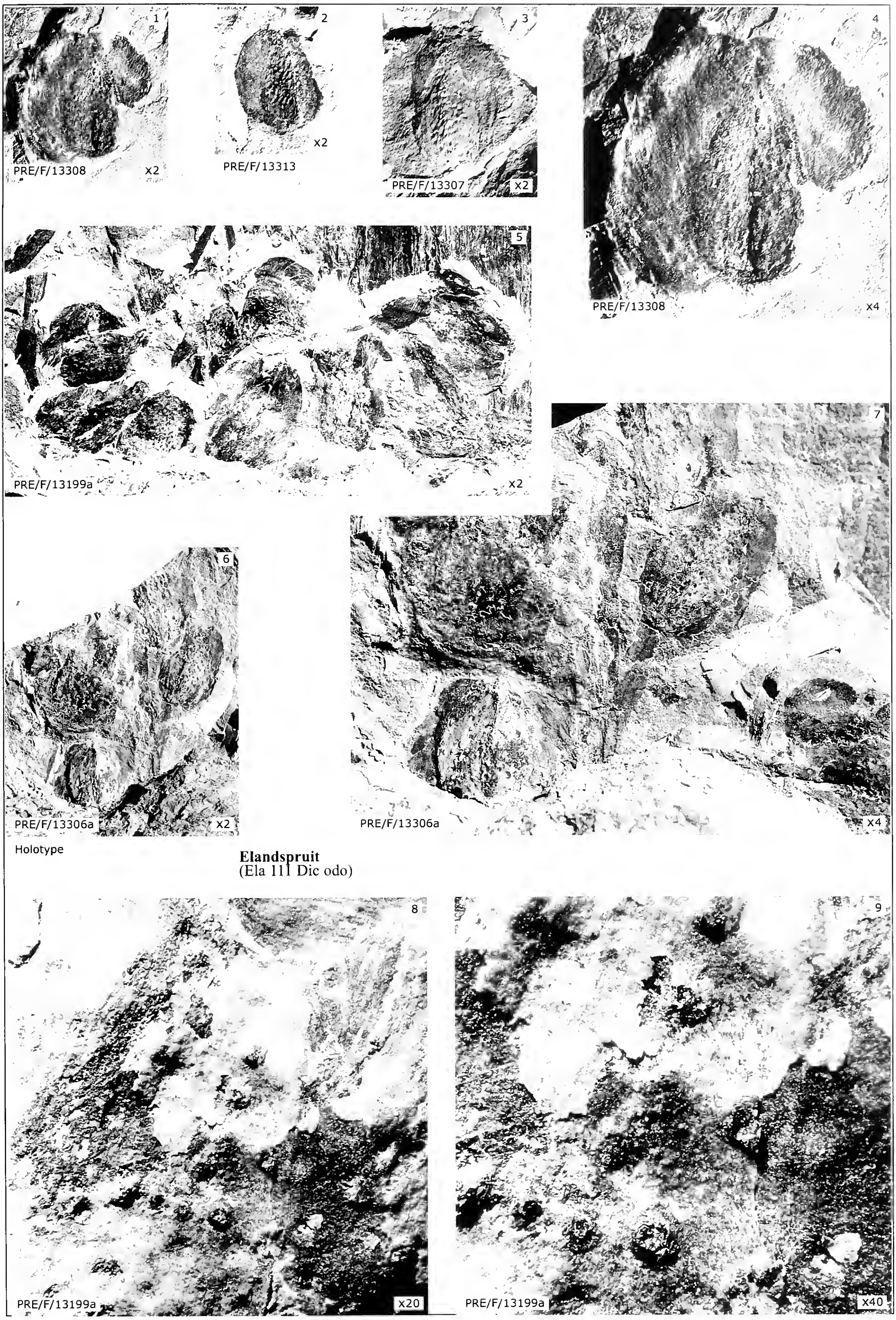

1
PRE/F/9442 x1
2
PRE/F/9440a x1
Holotype
Waldeck
(Wal 111 Dic odo)
3
PRE/F/9440a x2
4
PRE/F/9440a x4
5
PRE/F/9535b x1
6
PRE/F/9535a x1
7
BP/2/3325a x1
8
PRE/F/9535b x4
9
PRE/F/9538a x1
10
PRE/F/9538b x1



UMKOMASIALES pl. 101 *Fanerotheca waldeckiformis*



Fanerotheca cruciformis **pl. 102** **UMKOMASIALES**



Elandspruit
(Ela 111 Dic odo)

UMKOMASIALES **pl. 103** *Fanerotheca elandiformis*

GINKGOOPSIDA S.V.Meyen 1987
PETRIELLALES T.N.Taylor *et al.* 1994
KANNASKOPPIACEAE J.M.And. & H.M.And., fam. nov.

Kannaskoppia J.M.And. & H.M.And., gen. nov.

Type species
Kannaskoppia vincularis J.M.And. & H.M.And., sp. nov.
Kannaskop, Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis
A ginkgoopsid strobilus with a forked axis bearing rows of several simple megasporophylls consisting of a single cupule.

Generic characters
Fertile shoot: stem with short shoots in an irregular helical arrangement; leaves (1 or 2) and strobili (2 or 3) borne irregularly on each shoot.
Strobilus: lax, planar, bilaterally symmetrical, small (*ca* 20 mm long); axis gracile, proximally forked; megasporophylls in 2 adaxial oblique rows (of 4–6 units) along each fork (limb), angle between rows *ca* 90°.
Megasporophyll: apparently reduced to single pedunculate cupules; ovuliferous cupules recurved; peduncles 2–3 mm long, gracile, sinuously curved.
Cupule: small (*ca* 2.5 x 2 mm), roundly ovoid, splitting more or less regularly into 3 lobes at maturity.
Ovule/seed: unknown.

Etymology
Kannaskoppia—after the type locality Kannaskop, an Afrikaans name for a hill bearing *Canna* plants (monocots of the family Cannaceae).

Global range: 1 sp., Gondwana, Tr. (CRN).
First & last: Molteno Fm.

Gondwana Triassic occurrence
SAf—Karoo Basin, 1 TC (50 indivs).

Molteno occurrence (see Tab. 57)
Frequency (F): 1 TC (of 100 sampled in the Molteno).
Diversity (D): 1 species.
Abundance (A): 50 indivs; rare.

Kan 111 Ast spA: 50 indivs in 30 man-hrs cleaving (*ca* 20 per 1 man-day), rare

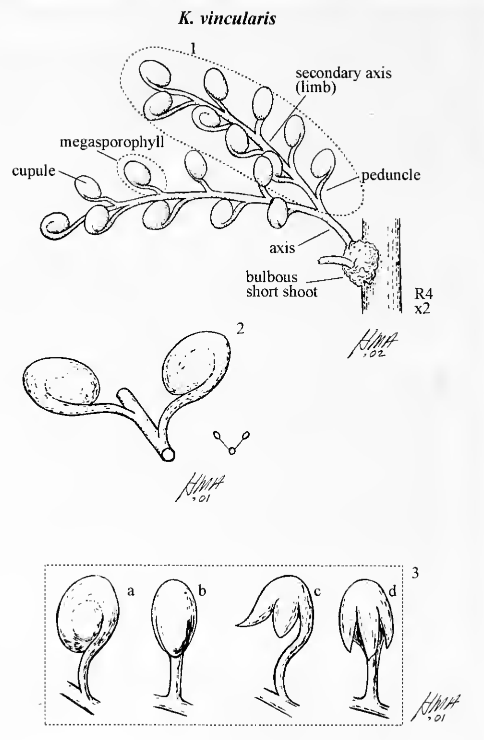
Affiliated organs
Male strobilus: *Kannaskoppianthus*—Grade 5 (Mor. corr., Kin. reinf.).
Foliage: *Kannaskoppifolia*—Grade 5 (Org. att.).

Classification & comparison
Suprageneric classification (Kannaskoppiaceae/Petriellales)

Kannaskoppia is considered here to be closely allied to *Petriellaea* and thus placed in the order Petriellales (Taylor *et al.* 1994). However, in view of the uncertainties that remain (see below), we include the Molteno genus in a distinct family, the Kannaskoppiaceae.

Intergeneric comparison (Gondwana Triassic)

Petriellaea is known from a single permineralised peat deposit in the Middle Triassic Fremouw Fm. of Antarctica (Taylor *et al.* 1994). The microscopic anatomy of the ovulate organ is exquisitely preserved revealing five ovules per cupule and many other details, but the overall architecture of the fruit remains uncertain. The reflexed cupules, as well as the size and configuration of the ovulate heads, are reminiscent of *Kannaskoppia*. It is possible that further new finds may show *Petriellaea* and *Kannaskoppia* to be congeneric, but this is not possible to conclude at the present time. What is known of the one genus is mostly unknown of the other.



tfs 1–3
based on full
reference palaeodeme

Reconstructions
Fertile shoot

The reconstructions (tfs 1–3 above; tfs 1, 2, p. 288) are based on the comprehensive palaeodeme from Kan 111 Ast spA. The shoot showing attachment of foliage and female fruit (p. 288, tf. 1) is largely a combination of PRE/F/13487a'y' and PRE/F/13487b'x'—the two portions of shoot illustrated on p. 289 (tfs 1, 2). These lie closely adjacent on the part and counterpart of a single cleaved slab. The arrangement of leaves and megasporophylls on the short shoots appears to show no consistent systematic pattern. However, the size and number of megasporophylls probably diminish towards the shoot apex.

Strobilus

The strobili, occurring in twos or threes, are found attached to bulbous short shoots which usually bear one or two leaves. Simplified reconstructions, with leaves removed, include a group of three strobili at natural size (p. 288, tf. 2), and a single strobilus showing characteristic fork and double row of megasporophylls at x2 magnification (tf. 1 above).

Megasporophyll

The megasporophyll is taken to consist of a single cupulate unit borne on a long gracile, slightly recurved peduncle. Cupule details (tfs 3a–d above) are based largely on three specimens, PRE/F/13489a,b, PRE/F/13508a,b and PRE/F/13518a,b; see pl. 105(1–3, 4), which show the cupules preserved at various angles. Due to the 3D nature of the preservation of the material shown in pl. 105(4), it is possible to observe the curved peduncle with its tendency to flex downwards, and to estimate the angle of *ca* 90° between the cupule rows as shown in our reconstructions (tfs 1, 2 above; tfs 1, 2, p. 288). The cupule is roundly ovoid and at maturity splits into three more or less regular lobes (tfs 3c–d above).

Ovule/seed

While much is known about the gross morphology of the megasporophylls and their mode of attachment, nothing is known of the interior organisation of the cupules or of the ovules. Nowhere on the many slabs bearing the fruit is there any indication that either cupules or seeds are individually dispersed.

assemblages (taphocoenosis)		*Kannaskoppifolia*	♀ *Kannaskoppia*	♂ *Kannaskopianthus*	microsporangia	man-hours cleaving	fruit abundance: indivs./man-day	♂ *K. lutinumerus*	" *K. matatiparvus*	" *K. irregularis*	" *K. telemagnus*
Cal 211	Hei elo	**5**	-	-	-	-	-	-	-	-	-
Gre 121	Hei elo	22	-	2	1	10	1/1	2	-	-	-
" 111	Equ sp	1	-	-	-	25	-	-	-	-	-
Boe 112	Dic cor	1	-	-	-	-	-	-	-	-	-
Cyp 111	Dic cra	83	-	-	-	100	-	-	-	-	-
Kan 112	Hei elo	19	-	5	1	15	3/1	5	-	5	-
" 111	Ast spA	**5**	50	-	-	30	20/1	-	-	-	-
Tel 111	Hei elo	33	-	4	1	90	1/2	2	-	-	2
Kom 111	Sph/Dic	30	-	2	1	10	2/1	-	-	2	-
Vin 111	Dic odo	2	-	-	-	-	-	-	-	-	-
Lut 311	Hei elo	66	-	16	-	50	3/1	16	-	-	-
Kon 211	Ast 2spp	4	-	-	-	-	-	-	-	-	-
Pen 311	Hei elo	41	-	-	-	35	-	-	-	-	-
" 411	" "	70	-	4	-	70	1/2	4	-	-	-
Kap 111	Dic spp	6	-	-	-	65	-	-	-	-	-
Nuw 111	Dic zub	1	-	-	-	21	-	-	-	-	-
Win 111	Hei elo	4	-	-	-	20	-	-	-	-	-
Hla 213	Dic elo	7	-	-	-	60	-	-	-	-	-
Umk 111	Dic 2spp	42	-	-	-	400	-	-	-	-	-
San 111	Dic cra	3	-	-	-	30	-	-	-	-	-
Mat 111	Dic dub	**2**	-	3	-	65	1/2	-	3	-	-
Lit 111	Dic/Hei	56	-	9	2	550	1/6	9	-	-	-
Aas 111	Hei elo	**2**	-	21	5	40	5/1	21	-	-	-
" 211	" "	19	-	1	-	35	1/3	1	-	-	-
" 311	" "	20	-	4	1	140	1/3	4	-	-	-
" 411	Dic/Sph	150	-	21	4	512	1/3	21	-	-	-
Total TCs		26	1	12	8			10	1	2	1
Total individuals		%	50	92	16			80	3	7	2

Tab. 57. *Kannaskoppia/Kannaskoppifolia*, Molteno occurrence

Evidence for affiliation of organs

Organic attachment

The holotype specimen of *Kannaskoppifolia vincularis*, together with the associated specimen on the same slab and additional material, constitutes the most convincing example of affiliated organs in the Molteno flora. Typical strobili and leaves are found attached to short shoots borne on a section of stem. Other specimens in the collection show the male strobilus, *Kannaskoppianthus*, attached in a similar manner to short shoots with *Kannaskoppifolia* leaves.

Comparisons beyond Gondwana Triassic

Apart from *Petriellaea*, the Mesozoic ovulate structure most comparable with *Kannaskoppia* is *Caytonia* (Jurassic, Eurasia)—in its size and form with lateral rows of dorsally reflexed cupules on short peduncles. In both genera the cupules fully enclose the ovule(s), but in *Kannaskoppia* their nature remains unknown. *Kannaskoppia* differs most evidently in the strobilus being forked and in the pedunculate cupules not abscising.

Caytonia (Jurassic/Eurasia)

Geographic & stratigraphic distribution: The ovulate organ, *Caytonia*, is now known as a widespread element of the lower half of the Jurassic of Eurasia: Yorkshire (>9 localities, M. Jurassic, Bajocian to Bathonian); Greenland (2 localities, basal Liassic, Hettangian); Poland (1 locality, U. Liassic); Sardinia and the USSR. Foliage identified as *Sagenopteris* has been reported from the U. Triassic to U. Cretaceous. More recently, the first report of *Caytonia* was made from Gondwana. Clifford & Camilleri (1998) describe *C. tierneyi* affiliated with *Sagenopteris* leaves from the Lower Jurassic Marburg Fm., Queensland, Australia.

Affiliation of organs: The *Caytonia* plant, the basis of the order Caytoniales, is one of around 20 fossil and extant gymnospermous 'orders' (or approximate ordinal groupings) on which recent cladistic analyses of the gymnosperms are based (Crane 1985, 1986, 1988). It is one of the few fossil gymnosperm genera where most organs are known through well-established affiliations (Grade 4) from a good number of localities. The organs include *Caytonia* (female strobilus), *Caytonanthus* (male strobilus) and *Sagenopteris* (foliage).

Preservation: Adding value to *Caytonia* (and affiliated organs) is that it is often found as well-preserved compressions.

Megasporophylls (morphology): 'Cupules' on short peduncles, spherical, reflexed dorsally with distinctive lip, apparently fleshy and berry-like at maturity, abscising at base of pedicel, with 8–30 tiny ovules.

Abundance: Explicit abundance and frequency data on fossil taxa are rarely given and this holds generally true for the *Caytonia* plant. In the Yorkshire Jurassic sites where it is best known, Harris (1964, p. 3) writes that it is 'by no means common'.

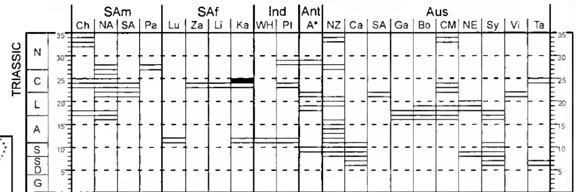
Diversity: No recent taxonomic revision of the *Caytonia* plant has been attempted, so any real sense of specific diversity is very difficult to gather. Five named species of the genus *Caytonia* appear to be currently valid.

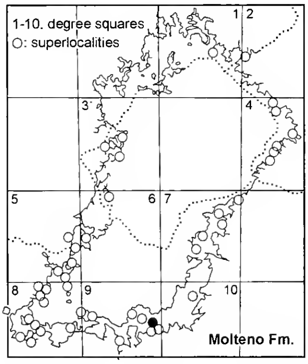
References: Harris (1933, 1940, 1958, 1964); Reymanówna (1973); Crane (1985); Krassilov (1977).

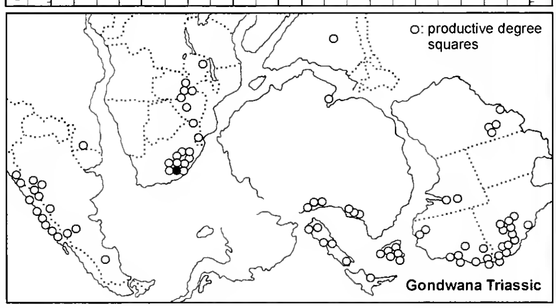
Polyspermophyllum (Permian/Argentina)

Kannaskoppia cupules are remarkably similar to the ovuliferous component of *Polyspermophyllum sergii* Archangelsky & Cuneo (1990) from the Permian of Argentina. These are described as 'distally placed curved ovuliferous units (cupules?) bearing a single ovule.' However, the ?cupules are borne on repeatedly dichotomising trusses and occur with attached leaves bearing a single medial vein and two longitudinal marginal furrows, setting them far apart from *Kannaskoppia*. *Polyspermophyllum* is included in the Dicranophyllales. Archangelsky & Cuneo also discuss the possible links of their genus to the Ginkgoales and other orders.

GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION








K. vincularis
1
R4
x1
tfs 1,2 based on
full reference palaeodeme,
but largely on
PRE/F/13487a'y' & PRE/F13487b'x'
2
R4
x2
Kan 111

Kannaskoppia vincularis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/13487 a'y'; tf. 2 below; pl. 104(3, 5).
Assemblage: Kan 111 Ast spA, Kannaskop.
Preservation: a shoot 90 mm long with clusters of foliage and megasporophylls attached; compressed 3D mould and cast (no cuticle or carbonised material); on the counterpart slab there is an additional isotype specimen, PRE/F/13487b'x', from which a piece of matrix can be lifted to reveal foliage and fruit at a different level; impression in thick-bedded, moderately baked, greenish grey silty mudstone with very poor cleavage.

Reference palaeodeme
Assemblage: as for holotype.
Specimens: *ca* 50 indivs, pls 104, 105 (includes further foliage as indicated);
- 5 torn sections of shoot with foliage and strobili attached;
- >50 detached strobili or clusters of strobili;
- 12 torn sections of shoot with foliage only;
- >25 detached leaves, generally torn or twisted.

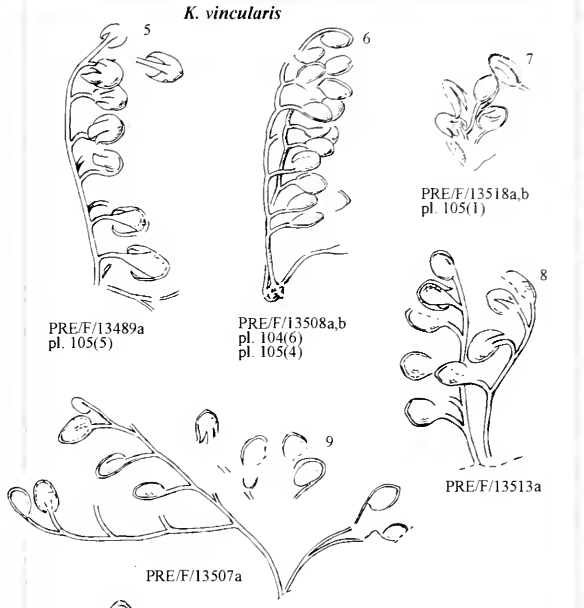
Sister palaeodemes—nil.

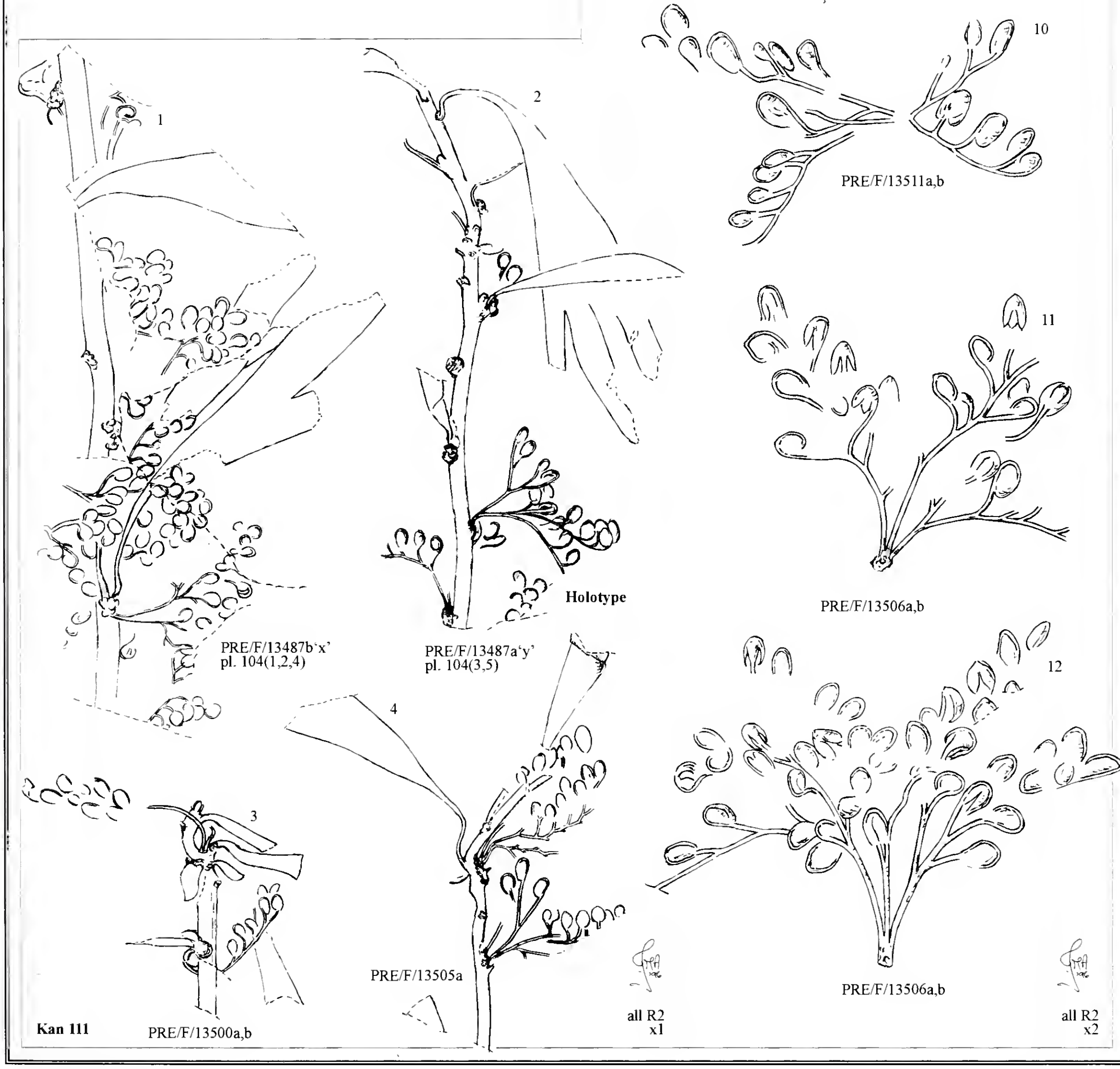
Specific diagnosis—as for genus.

Specific characters—as for genus.

Etymology
vincularis—*vinculum* (Lat.), link, bond, with reference to the fruit and foliage being found in organic connection at the type locality.

Comment & comparison—as for genus.





Kannaskoppianthus J.M.And. & H.M.And., gen. nov.

Type species
Kannaskoppianthus lutinumerus J.M.And. & H.M.And., sp. nov.
Lutherskop, Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis
A ginkgoopsid strobilus comprising a forked axis bearing rows of several simple microsporophylls, each with 5 longitudinal microsporangia in a concavity protected by an operculum.

Generic characters
Fertile shoot: strobili attached in fascicle with leaf cluster along shoot or at end of shoot.
Strobilus: lax, planar, bilaterally symmetrical, small (8–25 mm long) to rarely medium (up to 45 mm); axis gracile, proximally forked; microsporophylls in 2 adaxial oblique rows (of 8–10 units) along each fork (limb), angle between rows *ca* 90°.
Microsporophyll: spathulate, dorsiventrally flattened, bilaterally symmetrical; microsporangia 5 per unit, longitudinally aligned in distinctive concavity, attached distally to apical arcuate scale cap, protected by a dehiscent operculum.
Microsporangia: elongate-elliptic (1.5 x 0.5 mm), with fine linear ornamentation.
Pollen: unknown.

Etymology
Kannaskoppianthus—after the type locality and acknowledging certain affiliation with the female strobilus *Kannaskoppia*.

Global range: 4 spp., Gondwana, Tr. (CRN).
First & last: Molteno Fm.

Gondwana Triassic occurrence
SAf—Karoo Basin, 12 TCs (92 indivs).

Molteno occurrence
Frequency (F): 12 TCs (of 100 sampled in Molteno).
Diversity (D): 4 species.
Abundance (A): 92 indivs total; rare to extremely rare in top 8 TCs.

Aas 111 Hei elo:	21 indivs in	40 man-hrs	(5 per	1 man-day)	rare
Lut 311 Hei elo:	16 " "	50 "	(3 "	1 ")	"
Kan 112 Hei elo:	5 " "	15 "	(3 "	1 ")	"
Kom 111 Sph/Dic:	2 " "	10 "	(2 "	1 ")	"
Aas 411 Dic/Sph:	21 " "	512 "	(1 "	2 ")	very rare
Mat 111 Dic dub:	3 " "	65 "	(1 "	2 ")	" "
Tel 111 Hei elo:	4 " "	90 "	(1 "	2 ")	" "
Lit 111 Dic/Hei:	9 " "	550 "	(1 "	6 ")	extr. rare

The abundance figures reflected here for the eight TCs with the highest *Kannaskoppianthus* yield, account for every specimen found, no matter how fragmentary or poorly preserved. All were retained and curated. At the four further sites not listed above, *Kannaskoppianthus* is even rarer (Tabs 57, 58).

Although very rare, the *Kannaskoppianthus* male occurs in 12 of 25 TCs yielding *Kannaskoppifolia* foliage. This frequency ratio of 1:2 (male to foliage) is high for the Molteno. In the 12 TCs it ranges in abundance from 1 individual in 7 man-days cleaving to 5 in 1 day, with a norm at around 1 found every 2 days. There appears to be no particular pattern of abundance based on habitat.

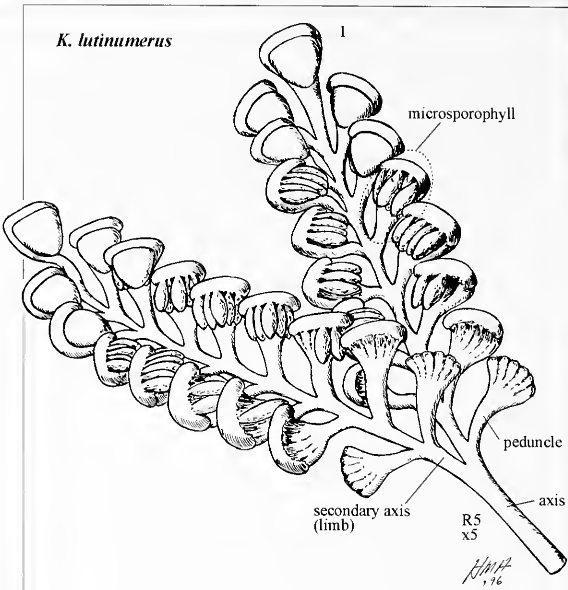
Affiliated organs
Female strobilus: *Kannaskoppia*—Grade 5 (Mor. corr.).
Foliage: *Kannaskoppifolia*—Grade 5 (Org. att.).

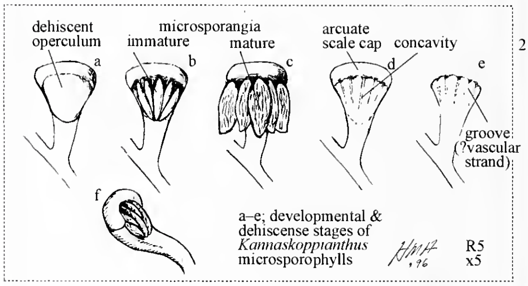
From Kommandantskop (Kom 111 Sph/Dic), PRE/F3231a,b (tf. 5 adjacent) shows two strobili of *Kannaskoppianthus* attached to an axis with a whorl of four *Kannaskoppifolia* leaves (see also tf. 2, p. 293). From Kannaskop (Kan 112 Hei elo), PRE/F/20114a,b (tf. 1, p. 293) shows a strobilus attached to a stem with leaf/branch scars. This is similar to the stems bearing leaves and female strobili (*Kannaskoppia*) from Kan 111 Ast. sp.A.

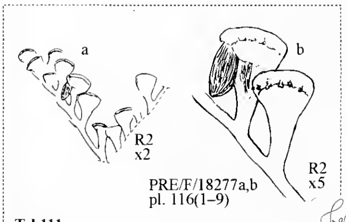
Classification & comparison
Suprageneric classification
See under *Kannaskoppia*.

Intergeneric comparison (Gondwana Triassic)
Kannaskoppianthus is unique among known ginkgoopsid microsporangiate genera. In their size, diagnostic forking and paired erect rows of fertile units, the micro- and megasporophylls (*Kannaskoppia*) are remarkably alike. The latter are noticeably more gracile.

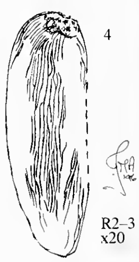
K. lutinumerus





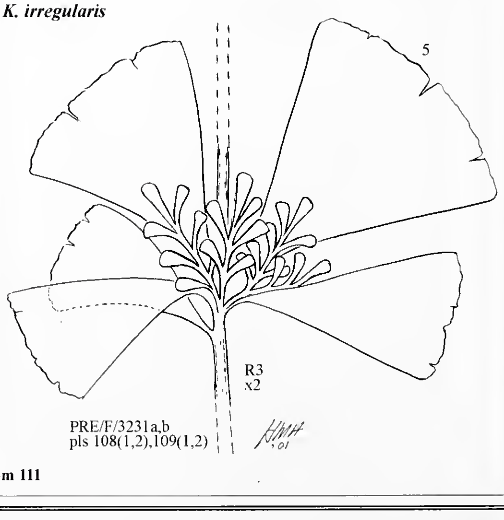


Tel 111



Aas 311
PRE/F/12001a,b
pl. 114(1,2)

K. irregularis



Kom 111

Reconstructions

The R5 reconstructions (tfs 1, 2 opposite) of *Kannaskoppianthus* are based on the full set of Molteno specimens at hand, but primarily on:

Lut 311; PRE/F/11433, pl. 110(3, 7): architecture of strobilus, nature of protective operculum
Aas 211; PRE/F/15280, pl. 113(1–4): angle of microsporophyll
Tel 111; PRE/F/18277a,b, pl. 116: structure of microsporophyll, attachment and number of microsporangia
Aas 411; PRE/F/12050 & 21720, pl. 115: attachment of microsporangia
Aas 311; PRE/F/12001, p. 290, tf. 4, pl. 114(1–3): morphology of microsporangia
Tel 111; PRE/F/7711, pl. 118: nature of protective operculum
Lit 111; PRE/F/21497: number of microsporangia, groove (?vascular strand)
Gre 121; PRE/F/7856: number of microsporangia, groove (?vascular strand)

Number of microsporangia

No specimens in the collection show microsporophylls with the full complement of five microsporangia attached. A specimen from Tel 111, PRE/F/18277a,b, clearly shows two attached microsporangia, pl. 116(1–9). The size and shape of these microsporangia suggest a full complement of five pollen sacs in the undehisced original. Furthermore, five grooves or vascular strands are seen where the microsporangia were probably attached (tf. 2d opposite).

Microsporophyll developmental & dehiscence stages (tfs 2 a–e opposite):

(a) microsporophyll with protective operculum covering the microsporangia;
(b) operculum dehisced revealing the 5 closely packed immature microsporangia;
(c) mature microsporangia ready to release pollen;
(d) microsporophyll with the microsporangia detached exposing 5 grooves or vascular strands;
(e) the woody arcuate scale cap is now detached; most specimens in the collection show this stage of preservation;
(f) microsporophyll at stage (b) in oblique view at characteristic angle (as if on intact strobilus).

Gondwana Triassic occurrence (elaborated)

A doubtful record of a sporophyll was reported by Jones & De Jersey (1947, tf. 59) from the Ipswich Basin in Australia. Although thought to bear seeds, in size and shape the specimen comes close to *Kannaskoppianthus*. However, poor preservation does not allow closer comparison.

Comparisons beyond Gondwana Triassic

The only pollen-bearing structures that show some similarity to *Kannaskoppianthus* occur in the Carboniferous of Euramerica. The class Lagenostomopsida includes the genera *Crossotheca* and *Feraxotheca*, both of which have numerous microsporangia attached at the end of modified ultimate pinnae. *Paracalathiops* shows a similarity in the basic architecture of a bifurcating axis and pedunculate microsporophylls (see Taylor & Taylor 1993).

While the megasporophyll *Kannaskoppia* shows some similarities to *Caytonia*, the microsporophyll *Kannaskoppianthus* differs greatly from *Caytonianthus*, which has a pinnate structure bearing lateral 'branches' and a few pedicellate microsporangia consisting of usually 'four locules' which dehisce towards their inner side (Crane 1985).

Intactness & preservation

Microsporangia (see Tab. 58)

The male strobilus has been found in 12 of the 25 *Kannaskoppifolia*-bearing TCs. Although microsporangia have been recognised from eight of these 12 TCs they remain notably rare, probably because the microsporangia are shed before or during fossilisation. Of the strobili preserved with associated microsporangia, only a small proportion are seen with sacs clearly attached: Tel 111 (PRE/F/18277a,b); Aas 411 (PRE/F/12050a,b, PRE/F/20558a,b, PRE/F/21339a,b, PRE/F/21720a,b). The best preserved of the individual microsporangia have been illustrated: pl. 114(1–5) from Aas 311, pl. 115(7) from Aas 411, and pl. 116(1–9) from Tel 111.

Pollen

Of all the *Kannaskoppianthus* microsporophyll sites, only the Lit 111 Dic/Hei TC yields carbonised compression material with the potential for extracting *in situ* pollen. And only two of the nine available strobili (PRE/F/5939 & PRE/F/5734) from this site appear to bear a few microsporangia that could possibly yield pollen.

Cuticles

Potential sample: Lit 111, 9 indivs.
Macerated (this work): 2 indivs.
Preservation grade: Grade 3 (fair), a few features available, small pieces mainly from stalk area.
Diagnostic characters: cells oblong to narrowly oblong, walls straight to gently curved; stomata absent; trichome bases apparently indicated by circular marks, distribution random but towards the end of cells, on both surfaces.
Comment: —
Significance:

Classification—The cuticular features do not indicate any particular plant group, but also do not dispute placement in the Ginkgoopsida and family Kannaskoppiaceae.

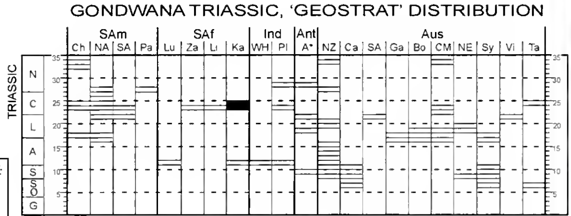
Affiliations—The diagnostic stomata and characteristic (?)glands found in the leaf (*Kannaskoppifolia*) cuticle have not been found in that of the affiliated male strobilus. The cell outlines and walls, however, correspond well with that characterising the foliage.

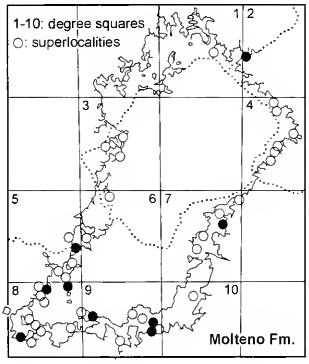
Adaptive radiation (Molteno diversity)

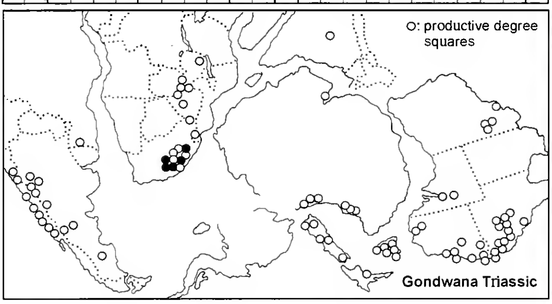
Evident diversity (four species) in the male fruit, *Kannaskoppianthus*, is clearly less than in the foliage where 10 species are recognised. (The female fruit is represented by only one species from one TC.) The diagnostic characters of the four male species lie in the size and forking of the strobilus and in the number of microsporophyll pairs per limb.

The Molteno species, based on the following TCs/palaeodemes, are mainly derived from *Heidiphyllum* thicket within Cycle 3.

K. lutinumerus—Lut 311 Hei elo (Lutherskop), 16 indivs
Heidiphyllum thicket; Cycle 3 (Mayaputi Member)
K. matatiparvus—Mat 111 Dic dub (Matatiele), 3 indivs
Dicroidium riparian forest (immature); Cycle 2 (Indwe Member)
K. irregularis—Kan 112 Hei elo (Kannaskop), 5 indivs
Heidiphyllum thicket; Cycle 3 (Mayaputi Member)
K. telemagnus—Tel 111 Hei elo (Telemachus Spruit), 2 indivs
Heidiphyllum thicket; Cycle 3 (Mayaputi Member)







Kannaskoppianthus lutinumerus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/11433a,b; pl. 110(3, 7, 9).
Assemblage (TC): Lut 311 Hei elo, Lutherskop.
Preservation: complete very clearly preserved strobilus, part and counterpart; impression in thickly laminated, medium grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 16 indivs, pl. 110(1–10).

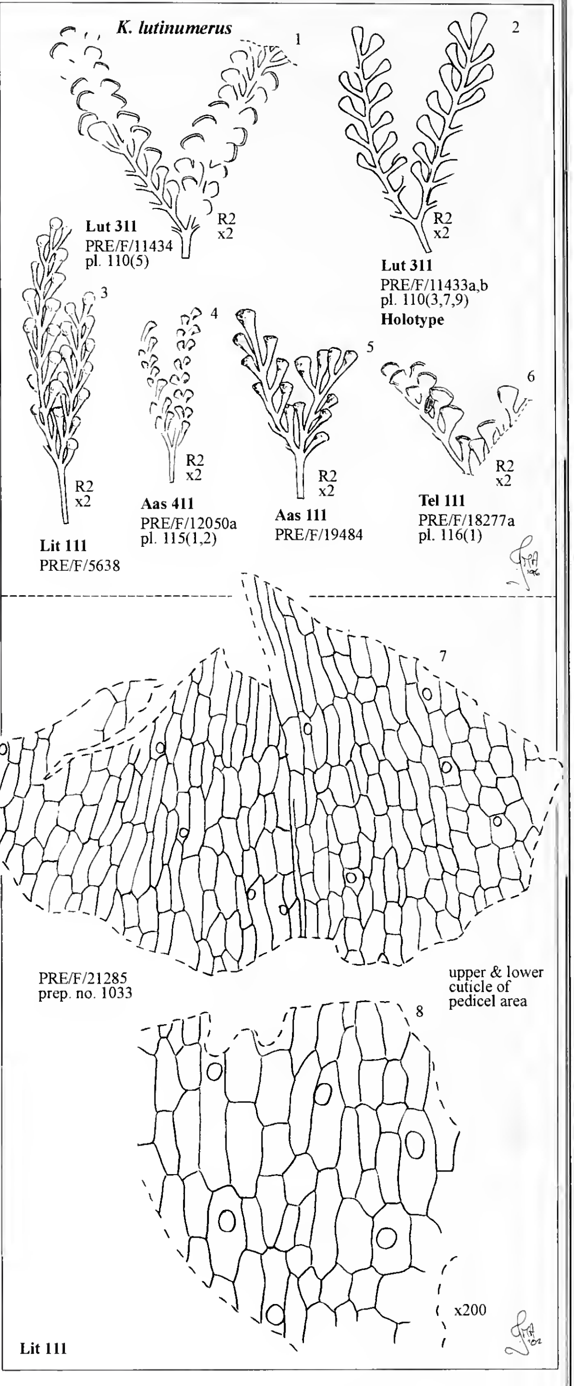
Sister palaeodemes—9 (best 6 listed)
Aas 111 Hei elo: 21 indivs (6 intact, 15 partial), highest yield (5 indivs/man-day).
Aas 411 Dic/Sph: 21 indivs (10 intact, 11 partial), microsporangia present.
Lit 111 Dic/Hei: 9 indivs (6 intact, 3 partial), cuticle, microsporangia present.
Aas 311 Hei elo: 4 indivs (1 intact, 3 partial), microsporangia present.
Tel 111 Hei elo: 2 indivs (1 intact, 1 isolated), microsporangia present.
Aas 211 Hei elo: 1 indiv. (intact), microsporangia present.

Specific diagnosis
A *Kannaskoppianthus* species with small once-forked strobili whose limbs bear 8–10 microsporophylls per row.

Specific characters
Attachment: unknown.
Strobilus: small (*ca* 16–18 mm long), regularly forked; microsporophylls 8–10 per row.
Microsporophyll: narrowly concavely conate (*ca* 1 mm wide distally).

Etymology
lutinumerus—*luti*, for the type locality Lutherskop; *numerus* (Lat.), with reference to the large number of microsporophylls per row.

Comment & comparison
This species is by far the most numerous and frequent of the four recognised in our Molteno collections. It is closely similar in form to *K. matatiparvus* but differs in its larger size and greater number of microsporophyll units per strobilus limb.



Kannaskoppianthus matatiparvus J.M.And. & J.M.And., sp. nov.

Holotype
Specimen: PRE/F/3205; pl. 114(10).
Assemblage (TC): Mat 111 Dic dub, Matatiele.
Preservation: intact strobilus, without counterpart; impression in thickly laminated, olive-grey shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 3 indivs (2 intact, 1 partial), pl. 114(8–10).

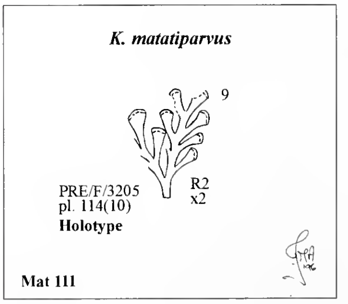
Sister palaeodemes—nil.

Specific diagnosis
A *Kannaskoppianthus* species with small once-forked strobili whose limbs bear 5 or 6 microsporophylls per row.

Specific characters
Attachment: unknown.
Strobilus: small (*ca* 8–10 mm long), regularly forked; microsporophylls 3–6 per row.
Microsporophyll: narrowly concavely conate (*ca* 1 mm wide distally).

Etymology
matatiparvus—*matati*, for the type locality Matatiele; *parvus* (Lat.), small.

Comment & comparison
K. matatiparvus is particularly rare (3 indivs) and infrequent (1 TC) and is differentiated from *K. lutinumerus* in the reduced number of microsporophyll units per limb.



Kannaskoppianthus irregularis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/20114a,b; pl. 117(1–6).
Assemblage (TC): Kan 112 Hei elo, Kannaskop.
Preservation: intact strobilus attached to an axis, part and counterpart; impression in very thin-bedded, moderately baked, medium grey shale with poor cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 5 indivs (1 intact, 4 partial), pl. 117(1–6).

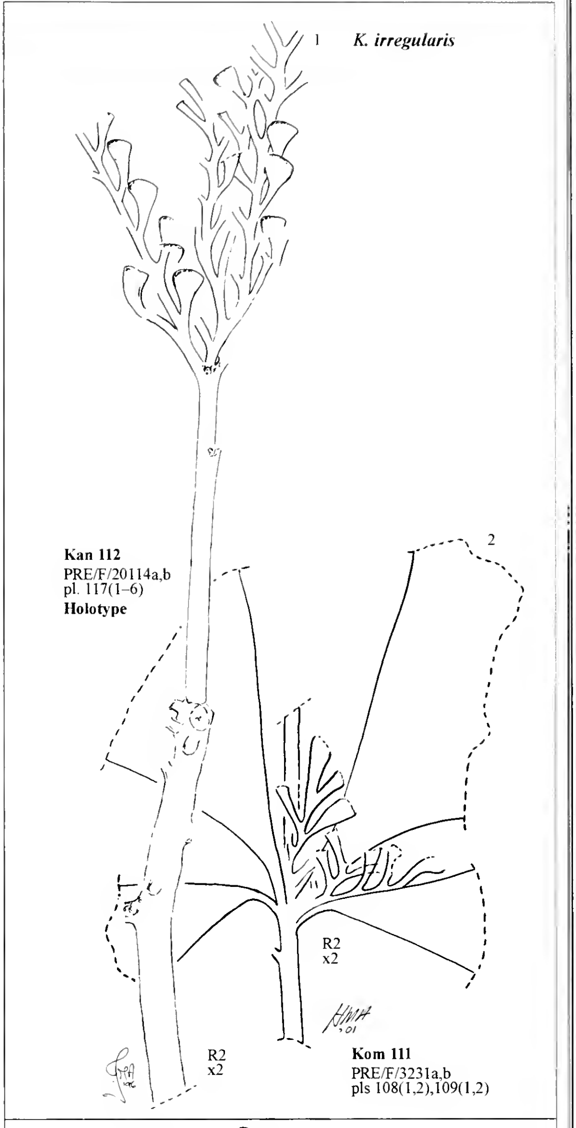
Sister palaeodemes—1 (as listed)
Kom 111 Sph/Dic: 2 indivs (1 partial, 1 fragm.), both attached to shoot with foliage), pls 108, 109.

Specific diagnosis
A *Kannaskoppianthus* species with medium-sized irregularly forked strobili whose limbs bear 5 or 6 microsporophylls per row.

Specific characters
Attachment: strobili attached terminally to a stem (?long shoot).
Strobilus: medium (>26 mm long), irregularly forked; microsporophylls 5 or 6 per row.
Microsporophyll: broadly concavely conate (*ca* 2 mm wide distally).

Etymology
irregularis—referring to the irregular branching of the strobilus.

Comment & comparison
K. irregularis differs from the other *Kannaskoppianthus* species in the irregularly branching strobili and in its mode of attachment. On the holotype, PRE/F/20114a,b, the stem shows leaf scars but no intact leaves. The specimen from Kom 111 (PRE/F/3231) consists of a stem with four attached leaves and two strobili that appear to be attached just below the bifurcation of their axes, i.e. showing no evidence of multiple branching (tf. 2). In size and shape this specimen is best placed in this species—but with uncertainty. The length of the strobilus may be much shorter than in the holotype, with only four pairs of microsporangia preserved as indicated in the reconstruction (p. 290, tf. 5).



Kannaskoppianthus telemagnus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/7711; pl. 118(1, 2, 4–6).
Assemblage (TC): Tel 111 Hei elo, Telemachus Spruit.
Preservation: almost complete strobilus, without counterpart; impression in thickly laminated, light olive-grey shale with poor cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 2 indivs (1 intact, 1 partial); pl. 118(1–6).

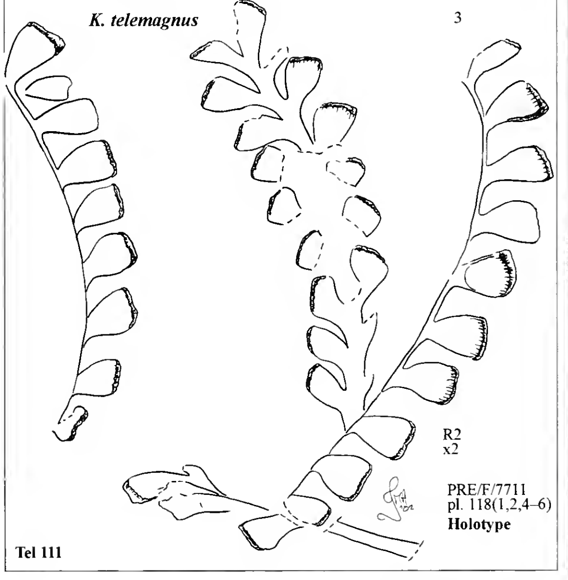
Sister palaeodemes—nil.

Specific diagnosis
A *Kannaskoppianthus* species with large strobili whose limbs bear 9 or 10 microsporophylls per row.

Specific characters
Attachment: unknown.
Strobilus: large (>40 mm long), fork unknown; microsporophylls 9 or 10 per row.
Microsporophyll: broadly convexly conate (*ca* 3 mm wide distally).

Etymology
telemagnus—with reference to the type locality Telemachus Spruit and to the large size of this species.

Comment & comparison
K. telemagnus differs strongly from the other three *Kannaskoppianthus* species in the far larger size of its strobili and microsporophylls. It is affiliated with the distinctive large-leaved *Kannaskoppifolia* sp.H (p. 297, tf. 2) which, with 30 individuals (from Tel 111), is quite common. Two specimens of *K. lutinumerus* have also been collected from this same Tel 111 TC.



Kannaskoppifolia J.M.And. & H.M.And., gen. nov.

Type species
Kannaskoppifolia vincularis J.M.And. & H.M.And., sp. nov.
Kannaskop, Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis
A ginkgoopsid leaf without distinct petiole and with cuneate to flabellate, entire to trifidly divided lamina with forking, subparallel anastomosing venation.

Generic characters
Attachment: leaves (1 or 2) and strobili (2 or 3) borne irregularly on short shoots.
Leaf: narrowly to broadly cuneate to flabellate; petiole not distinct; lamina entire to deeply segmented with few to numerous segments based on a trifid rather than bifid plan; veins fine, forking, radiating, subparallel and anastomosing to form a variously elongated mesh.
Cuticle: this vol., p. 296, tfs 1, 2.

Etymology
Kannaskoppifolia—referring to leaves from the Kannaskop locality.

Global range—many spp., Gondwana, Tr. (SCY–NOR).
First: *Kannaskoppifolia* (*Ginkgoites* sp.), (Walkom 1925a); L. Newport Fm., Turrimetta Head, Sydney, Australia.
Last: *Kannaskoppifolia* (*Chiropteris copiapensis*), (Solms-Laubach & Steinmann 1899); ?Fm., Quebr. La Ternera, Copiapo, Chile.

Gondwana Triassic occurrence
Frequency (F): 23 degree squares (of the 84 across Gondwana).
Ubiquity (U): 3 continents (of 5 comprising Gondwana).
Diversity (D): 10 foliage species.
Abundance (A): <1% (the norm in Molteno TCs).
Longevity (L): 26 myrs (Spathian to Upper Norian).
Colonisation success: FUDAL rating 23/3/10/–/26 = 62.
Intermediate success (Grade 3); *Kannaskoppifolia* was the 5th most prominent foliage genus in the Gondwana Triassic; it was ubiquitous, diverse, long-lived and relatively frequent, but generally lacking in abundance.
Endemism: certain species occur widely distributed on three continents, while at the other end of the scale, three species from the Molteno are single-assemblage endemics.

Molteno occurrence
Frequency (F): 25 TCs (of 100 sampled in the Molteno).
Diversity (D): 10 species.
Abundance (A): common (3–5%) in 2 TCs; occasional (2%) in 2 TCs; and <1% in the other 21 TCs.

Habit: possibly herbaceous pioneers, from erect shrublets to climbers.
Preferred habitat: occupied a wide range of habitats, but principally *Dicroidium* riparian forest, *Heidiphyllum* thicket and fern meadows of riverine sandbanks and floodplain wetlands.

Affiliated organs
Female strobilus: *Kannaskoppia*—Grade 5 (Org. att.).
Male strobilus: *Kannaskoppianthus*—Grade 5 (Org. att.).

Classification & comparison
Suprageneric classification
As this is an attached leaf, the classification is based on the ovulate strobilus *Kannaskoppia* (p. 286).

Intergeneric comparison
Such leaves were frequently classified as *Chiropteris* or *Ginkgoites* prior to Retallack (1980a) placing them in *Ginkgophytopsis*. In view of the proven affiliation of attached leaves with male and female strobili occurring in the Molteno, we here erect the new genus *Kannaskoppifolia*. We suggest that *Ginkgophytopsis* be restricted to Devonian and Carboniferous leaves as dealt with by Høeg (1967), who included the genus in the order Palaeophyllales.

Other reticulate leaves from the Molteno, such as *Gontriglossa, Graciliglossa* and *Cetiglossa*, all have a distinct midrib similar to that in *Glossopteris* (Permian) and *Sagenopteris* (Jurassic) leaves.

Eoginkgoites Bock from the Upper Triassic Newark Group and the Chinle Fm., USA (Ash 1976, 1977) has anastomosing venation and syndetocheilic stomata, but differs in the finer venation, a marginal vein, pinnate form and its papillate cuticle. Ash (1976, p. 1329) suggests a relationship with the Bennettitales rather than the Ginkgoales.

Gondwana Triassic (elaborated)
Kannaskoppifolia is a widespread element throughout the Gondwana Triassic. It is recorded in the literature from eight 'localities' (*ca* 88 indivs illustrated) in S. America (Chile, N. Argentina, S. Argentina) and 15 'localities' in Australasia (Queensland, NSW, Victoria, South Australia and New Zealand). Many of the published illustrations are insufficiently clear to show whether the venation anastomoses or not. In such instances one might be confusing this genus with *Sphenobaiera*, which can appear superficially similar (especially where specimens tend towards a bifurcating rather than trifurcating division of the lamina). The abundance of *Kannaskoppifolia* is rarely, if ever, clearly stated in the literature. The general impression is that it is uncommon, as in the Molteno.

Recent literature (adding to above text)
Since virtually completing our manuscript, two papers directly relevant to *Kannaskoppifolia* have appeared: Herbst *et al.* (2001), Barone-Nugent *et al.* (2003, in press).

Herbst *et al.* (2001) erect the new genus *Rochipteris* for 'some Gondwanic leaf species previously assigned to *Chiropteris* Kurr ex Bronn'. They describe five species of *Rochipteris*, two being new, from the Upper Triassic of Argentina and Chile. *Kannaskoppifolia* should likely become a junior synonym of *Rochipteris*. However, the South American foliage apparently yields no cuticle and there is no mention of female or male fruit affiliates.

Barone-Nugent *et al.* (in press) adopt the name *Rochipteris* for two new species and a third unnamed species from the Ipswich Coal Measures, the Leigh Creek Coal Measures and the Springfield Basin of the Upper Triassic of eastern Australia. As for the South American material, there occurs no affiliated fruit such as described here from the Molteno, but cuticle is illustrated and described for the Leigh Creek species, *R. amplexicaulis*. This cuticle is, in many respects, very different from that which we find characterising the Molteno species. In particular, the stomata appear not to be transverse and the cells are isodiametric (almost square over the veins), not oblong. Furthermore, there are six subsidiary cells and these are clearly lappetate. The Molteno stomata are paracytic and nonlappetate. However, certain specialised cells (trichomes or glands) are remarkably similar. The leaf morphology of *R. amplexicaulis*, with its markedly expanded clasping base, is likewise rather different from the Molteno *Kannaskoppifolia* species. We suggest that this species, at least, may be better placed in a new genus within the family Kannaskoppiaceae.

Kannaskoppifolia vincularis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/13521; pl. 106(1).
Assemblage (TC): Kan 111 Ast sp.A, Kannaskop.
Preservation: a portion of shoot with leaves attached, without counterpart; impression, in thick-bedded, moderately baked, greenish grey silty mudstone with very poor cleavage.

Reference palaeodeme
Assemblage (TC): Kan 111 Ast sp.A, Kannaskop.
Specimens: 5 sections of shoot with foliage and megasporophylls attached; 12 sections of shoot with foliage only; >25 detached leaves, generally torn or twisted (pls 104, 106, 107).

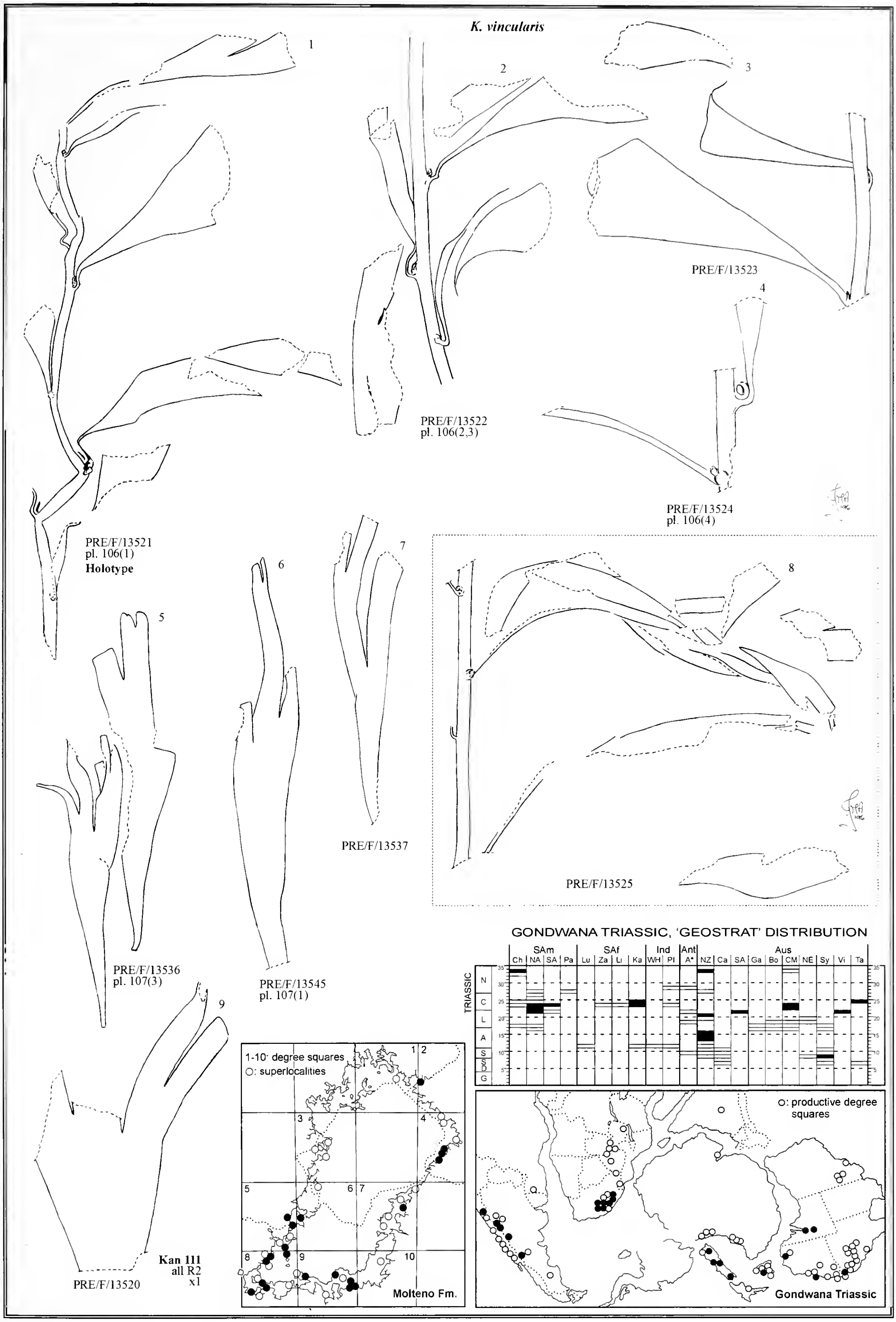
Sister palaeodemes—nil.

Specific diagnosis
A *Kannaskoppifolia* species, found attached to a shoot, with entire to partly segmented narrowly wedge-shaped lamina.

Specific characters
Attachment: leaves on long shoots (?new shoots) in irregular helical arrangement; leaves on short shoots in fascicle with female strobili.
Leaf: narrowly wedge-shaped, of medium size (up to 70 x 20 mm); lamina entire to partly divided into 3 or more segments; base sharply angled.

Etymology
vincularis—*vinculum* (Lat.), link, bond, with reference to the fruit and foliage being found in organic connection at the type locality.

Comment & comparison
This species is similar in shape and size to leaves previously described as *Ginkgophytopsis lacerata* by Retallack (1983), but the latter have not been found attached.


K. vincularis
1
2
3
PRE/F/13523
4
PRE/F/13522
pl. 106(2,3)
PRE/F/13524
pl. 106(4)
PRE/F/13521
pl. 106(1)
Holotype
5
6
7
8
PRE/F/13537
PRE/F/13525
PRE/F/13536
pl. 107(3)
PRE/F/13545
pl. 107(1)
9
Kan 111
all R2
x1
PRE/F/13520
GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION
SAm
SAf
Ind
Ant
Aus
Ch NA SA Pa Lu Za Li Ka WH Pl A* NZ Ca SA Ga Bo CM NE Sy Vi Ta
TRIASSIC
N
C
L
A
S
S
D
G
1-10' degree squares
○: superlocalities
Molteno Fm.
○: productive degree squares
Gondwana Triassic

Cuticles

Potential sample: Lit 111, 51 indivs; Umk 111, 42 indivs.

Macerated (this work): Lit 111, 35 indivs; Umk 111, 30 indivs; only a few indivs yielded good cuticle.

Preservation grade: Grade 4, features clear, fair-sized pieces.

Diagnostic characters: cells isodiametric to oblong (linear over vein areas), walls gently curved; stomata hypostomatic, nonpapillate, interveinal, transversely orientated; subsidiary cells paracytic, non-cutinised, nonlappetate, guard cells narrowly elliptic; specialised cells isodiametric to circular, strongly cutinised.

Comment: The specialised cells may be trichome bases or, in appearing strongly cutinised, glands. They occur scattered on the upper and lower cuticle. Such cells have not previously been recorded from the Molteno.

Significance

Classification—The transversely orientated, paracytic stomata make the cuticle of *Kannaskoppifolia* quite unique amongst the Ginkgoopsida. The only other taxon with clear paracytic stomata in the Molteno is *Gontriglossa verticillata* placed in the Gnetopsida. The latter has digitate amorphous cells and the stomata are orientated randomly in the interveinal areas.

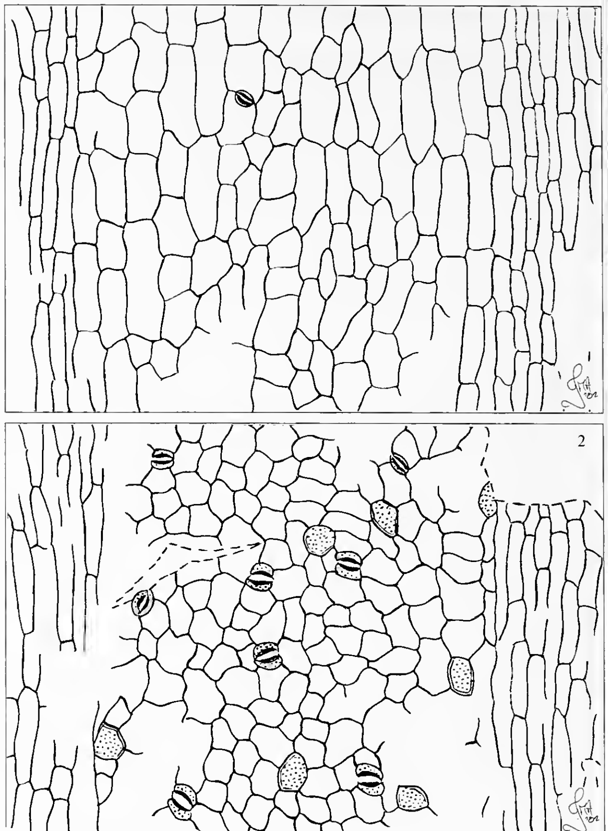
The different species of *Kannaskoppifolia* from Lit 111 and Umk 111 all exhibit distinctive cuticles. That from the single specimen of *K. vincularis* from Lit 111 is used here to illustrate the generic characteristics. The second species, *K.* sp.F from Lit 111, and *K.* sp.E from Umk 111 both show papillate epidermal cells. While the other common species from Umk 111, *K.* sp.C, has yielded only poorly preserved cuticle, it does show the diagnostic stomata and specialised cells. The remaining two species (each represented by one individual) yield potential cuticle but have not been macerated or studied.

Affiliations—Cuticular correspondence between the leaf and male strobilus is not clear on present evidence and affiliation is based on direct attachment.

Adaptive radiation (Molteno species, see text on p. 23).

We currently recognise 10 species of *Kannaskoppifolia* (Tab. 58) as illustrated here (only the type species is described). Very interestingly, the species in many instances coincide with different habitats, suggesting that they are biologically and ecologically distinct entities.

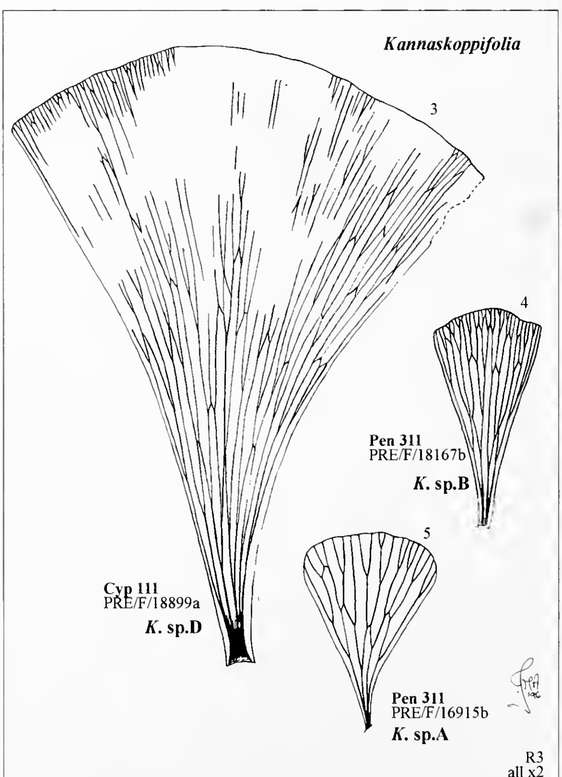
K. vincularis upper 1

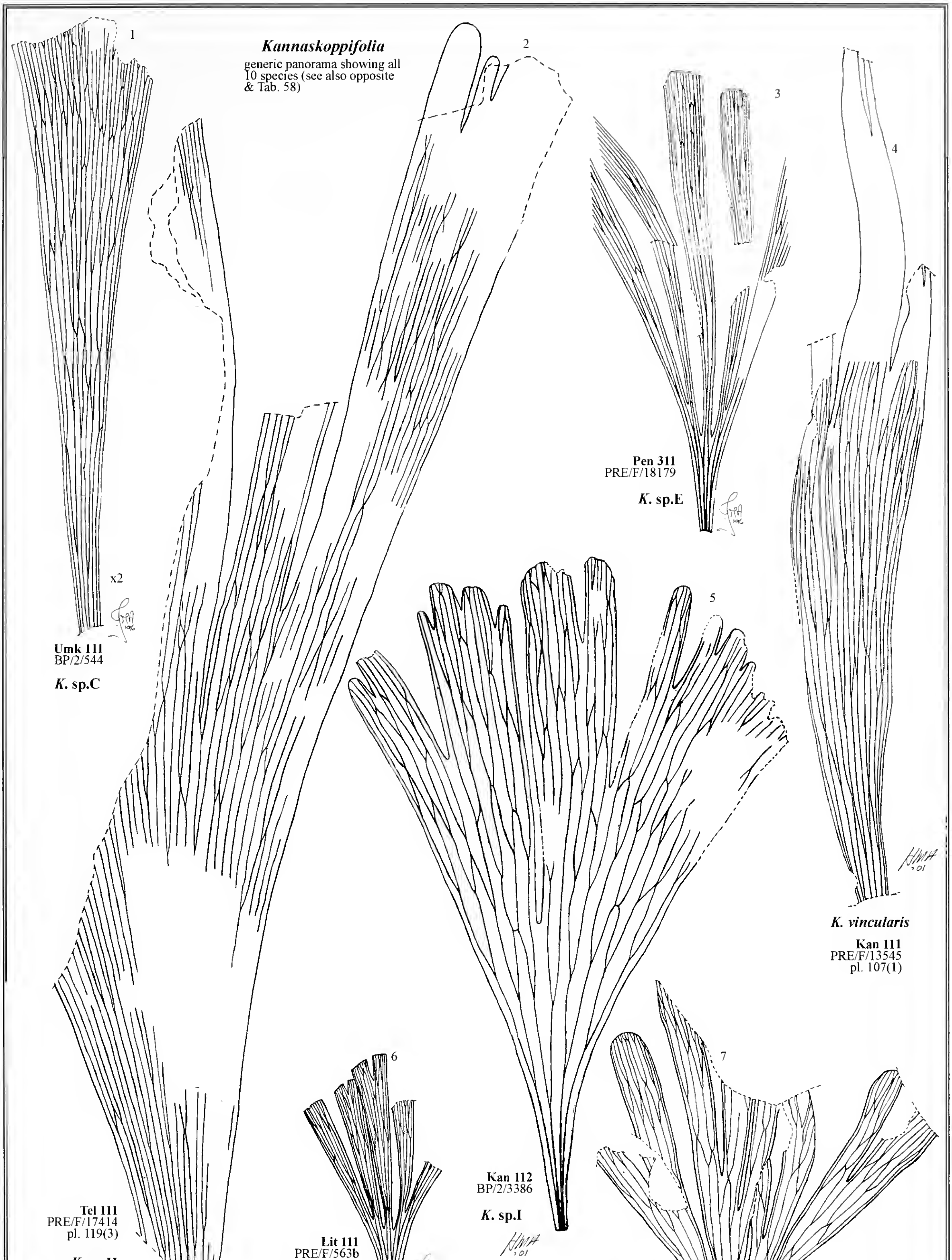


Lit 111 PRE/F/5641 lower x100
prep. no. 973

assemblages (taphocoenosis)	*Kannaskoppifolia*	*K.* sp.A (Pen 311) 1	" sp.B (Pen 311) 2	" sp.C (Umk 111) 3	" sp.D (Cyp 111) 4	" sp.E (Pen 311) 5	" sp.F (Lit 111) 6	" sp.G (Umk 111) 7	" *vinc.* (Kan 111) 8	" sp.H (Tel 111) 9	" sp.I (Kan 112) 10	" spp. indet	♀ *Kannaskoppia*	♂ *Kannaskoppianthus*
Cal 211 Hei/Ast	**5**	-	-	-	-	-	-	-	**5**	-	-	-	-	-
Gre 121 Hei elo	22	-	-	-	-	22	-	-	-	-	-	-	-	2
" 111 Equ sp	1	-	-	-	-	-	-	-	-	-	-	1	-	-
Cyp 111 Dic cra	83	-	-	-	80	-	1	-	2	-	-	-	-	-
Boe 112 Dic cor	1	1	-	-	-	-	-	-	-	-	-	-	-	-
Kan 112 Hei elo	19	1	2	-	-	10	-	-	-	2	4	-	-	5
" 111 Ast spA	**5**	-	-	-	-	-	-	-	**5**	-	-	-	50	-
Tel 111 Hei elo	33	1	2	-	-	-	-	-	-	30	-	-	-	4
Kom 111 Sph/Dic	30	-	-	-	29	-	1	-	-	-	-	-	-	2
Vin 111 Dic odo	2	-	-	-	-	-	-	-	2	-	-	-	-	-
Lut 311 Hei elo	66	-	-	-	66	-	-	-	-	-	-	-	-	16
Kon 211 Ast 2spp	4	-	-	-	-	4	-	-	-	-	-	-	-	-
Pen 311 Hei elo	41	2	5	-	-	34	-	-	-	-	-	-	-	-
" 411 Hei elo	80	-	10	-	-	70	-	-	-	-	-	-	-	4
Kap 111 Dic/Ris	6	-	-	-	-	6	-	-	-	-	-	-	-	-
Nuw 111 Dic zub	1	-	-	-	1	-	-	-	-	-	-	-	-	-
Win 111 Hei elo	4	-	-	-	1	3	-	-	-	-	-	-	-	-
Hla 213 Dic elo	7	-	-	-	-	2	4	-	1	-	-	-	-	-
Umk 111 Dic 2spp	42	-	-	19	-	21	-	1	1	-	-	-	-	-
San 111 Dic cra	3	-	-	-	-	2	1	-	-	-	-	-	-	-
Mat 111 Dic zub	**2**	-	-	-	-	-	17	-	**2**	-	-	-	-	3
Lit 111 Dic/Hei	56	-	-	-	-	-	55	-	1	-	-	-	-	9
Aas 111 Hei elo	**2**	-	-	-	-	**2**	-	-	-	-	-	-	-	21
" 211 Hei elo	19	-	-	-	-	18	-	-	1	-	-	-	-	1
" 311 Hei elo	26	-	-	-	-	25	-	-	1	-	-	-	-	4
" 411 Dic/Sph	150	-	-	-	-	150	-	-	-	-	-	-	-	21
Total TCs	26	4	4	1	5	14	6	1	10	2	1	1	1	12
Total individuals	%	5	19	19	177	%	79	1	%	32	4	1	50	92

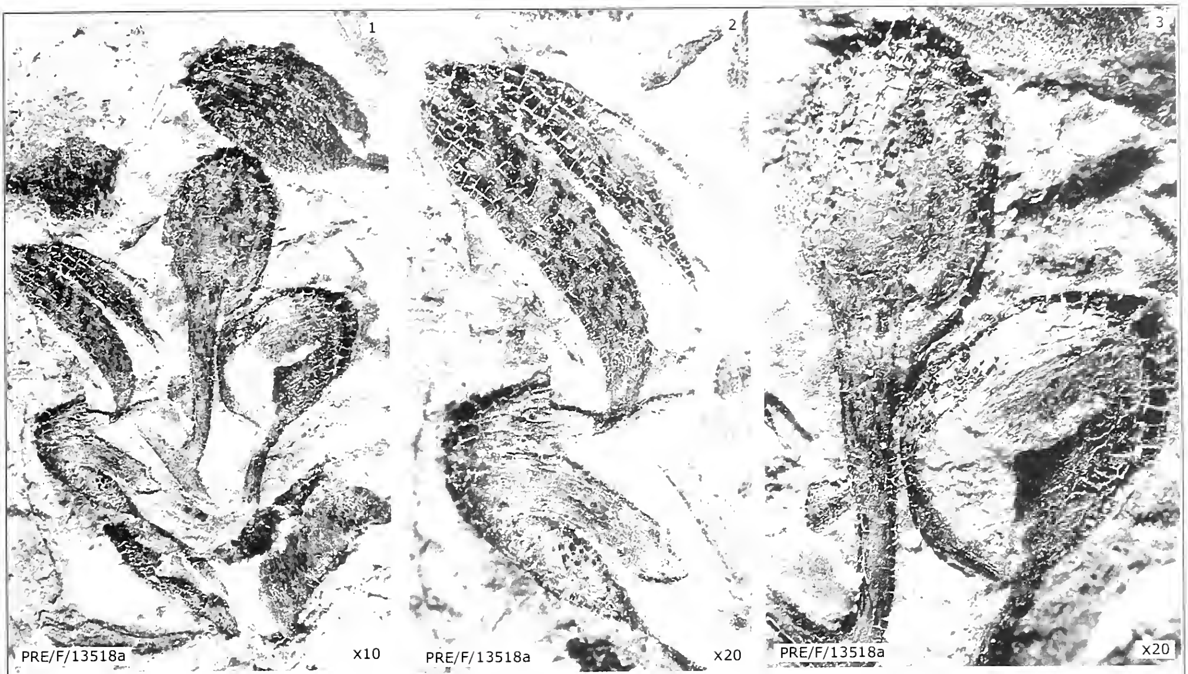
Tab. 58. ***Kannaskoppifolia*, Molteno occurrence**



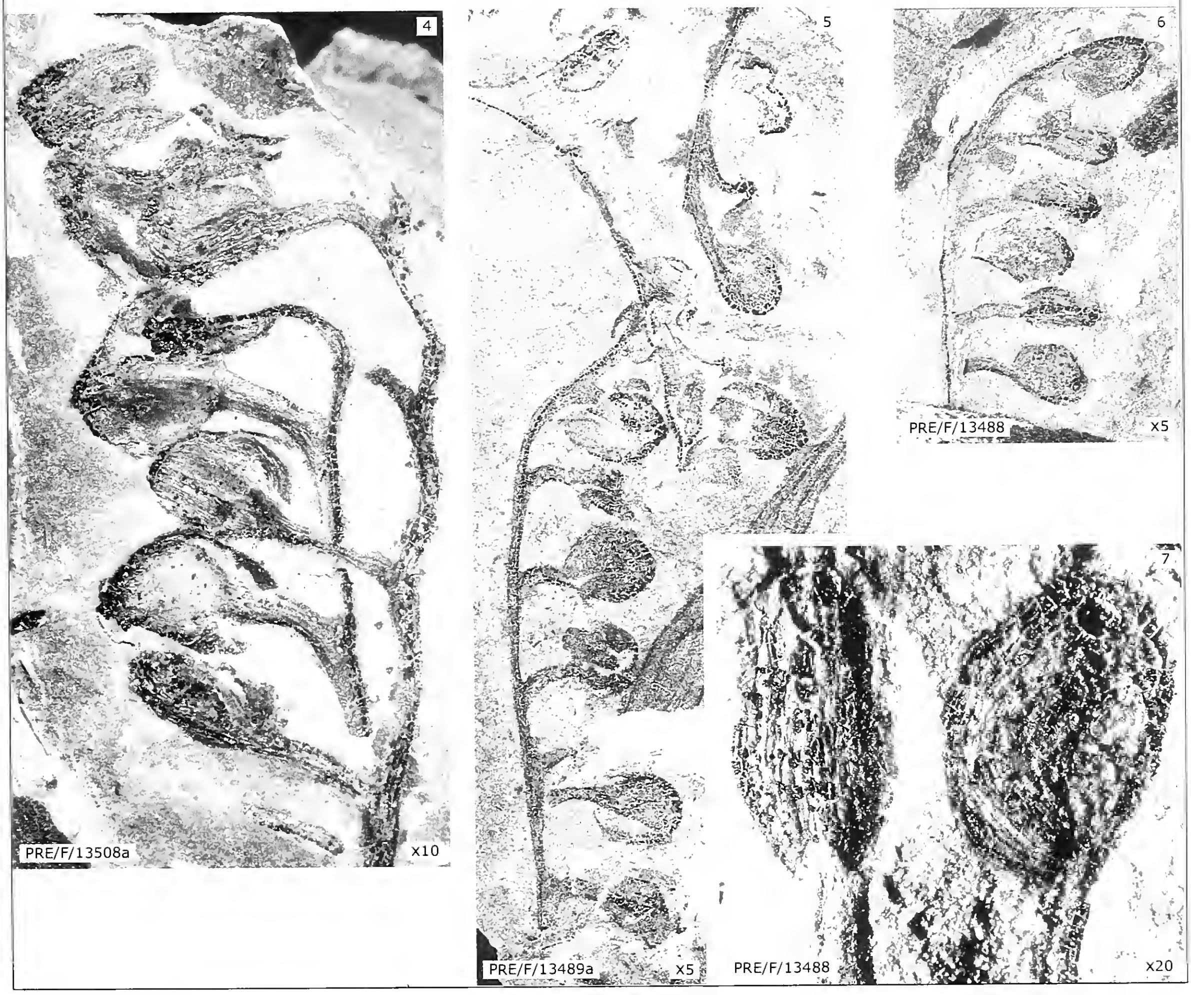


Kannaskoppifolia
generic panorama showing all 10 species (see also opposite & Tab. 58)
1
x2
Umk 111
BP/2/544
K. sp.C
2
Tel 111
PRE/F/17414
pl. 119(3)
K. sp.H
3
Pen 311
PRE/F/18179
K. sp.E
4
K. vincularis
Kan 111
PRE/F/13545
pl. 107(1)
5
Kan 112
BP/2/3386
K. sp.I
6
Lit 111
PRE/F/563b
K. sp.F
7
Umk 111
BP/2/539
K. sp.G
all R3
x2

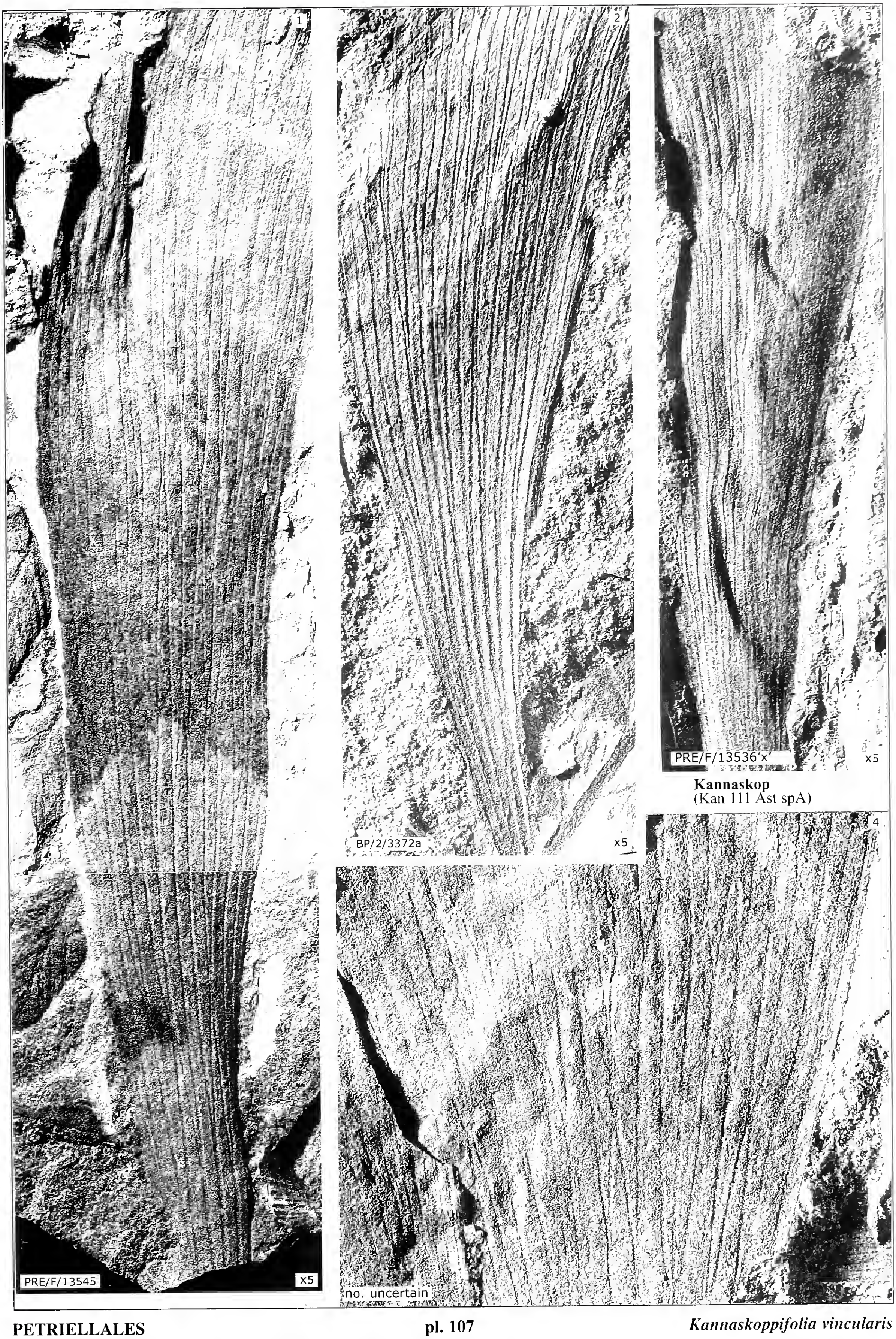

1
PRE/F/13487b'x'
x1
2
PRE/F/13487b'x'
x1
3
PRE/F/13487a'y'
x1
Kannaskop
(Kan 111 Ast spA)
Holotype
4
PRE/F/13487b'x'
x2
5
PRE/F/13487a'y'
x2
6
PRE/F/13508a
x5

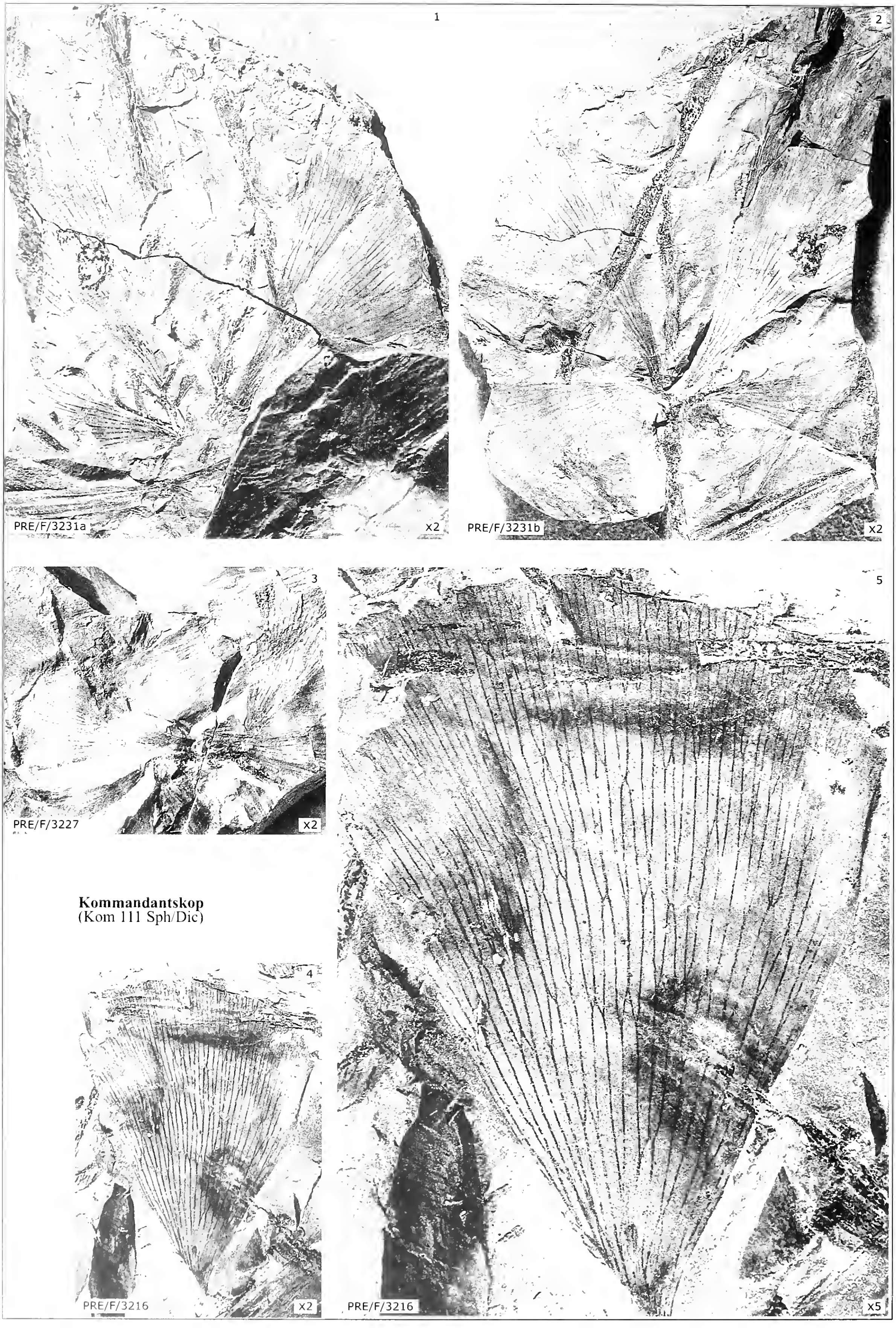


Kannaskop
(Kan 111 Ast spA)



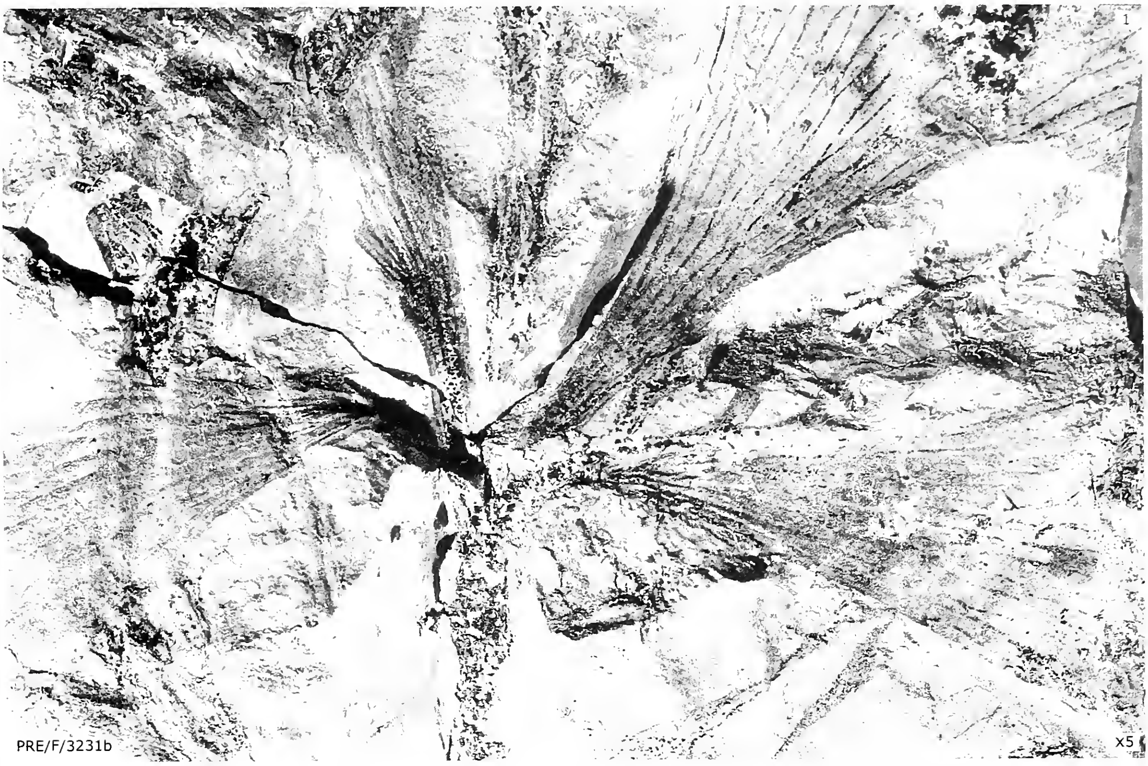
Kannaskop
(Kan 111 Ast spA)


1
PRE/F/13545
x5
2
BP/2/3372a
x5
3
PRE/F/13536'x'
x5
Kannaskop
(Kan 111 Ast spA)
4
no. uncertain

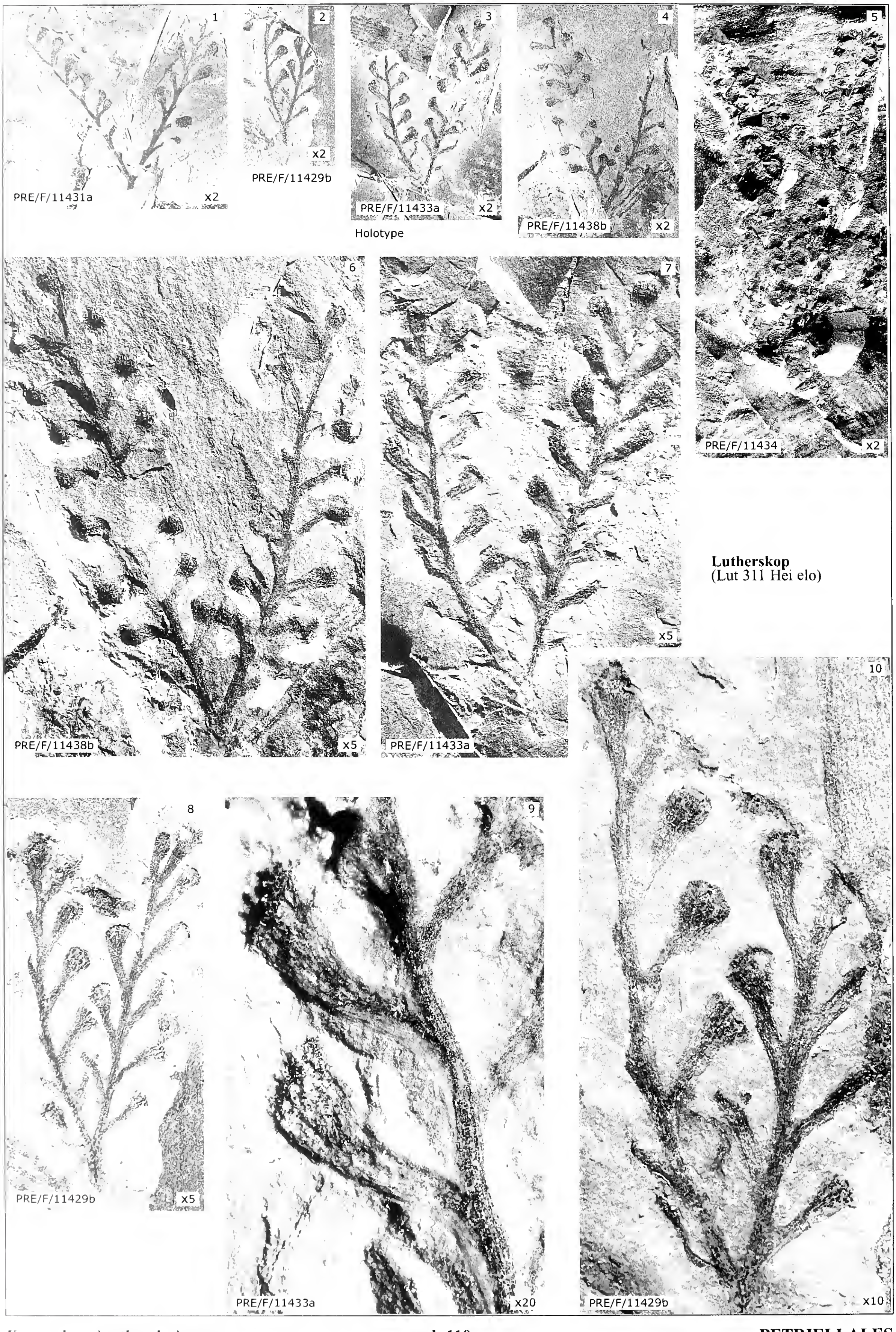


Kommandantskop
(Kom 111 Sph/Dic)

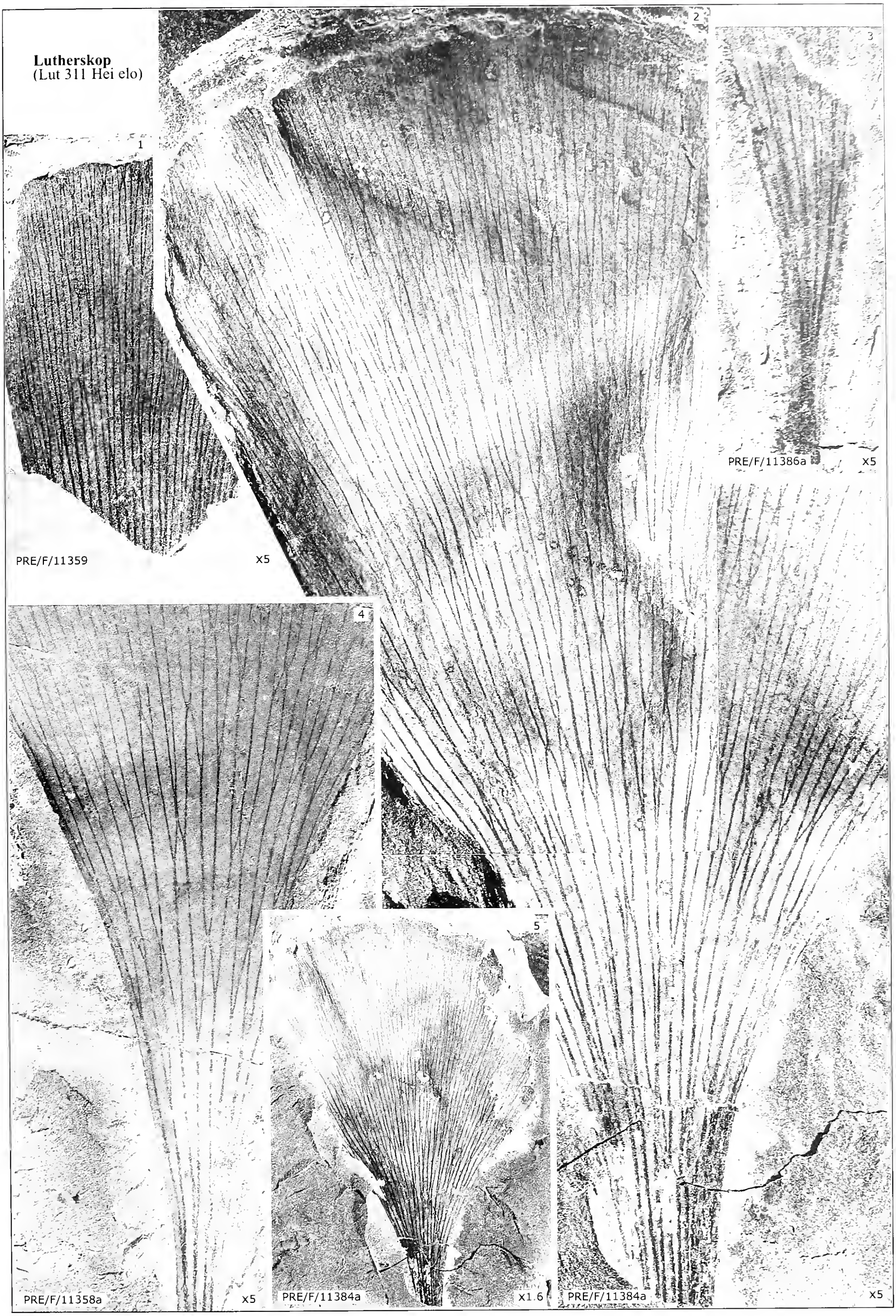
Kannaskoppianthus irregularis **pl. 108** **PETRIELLALES**



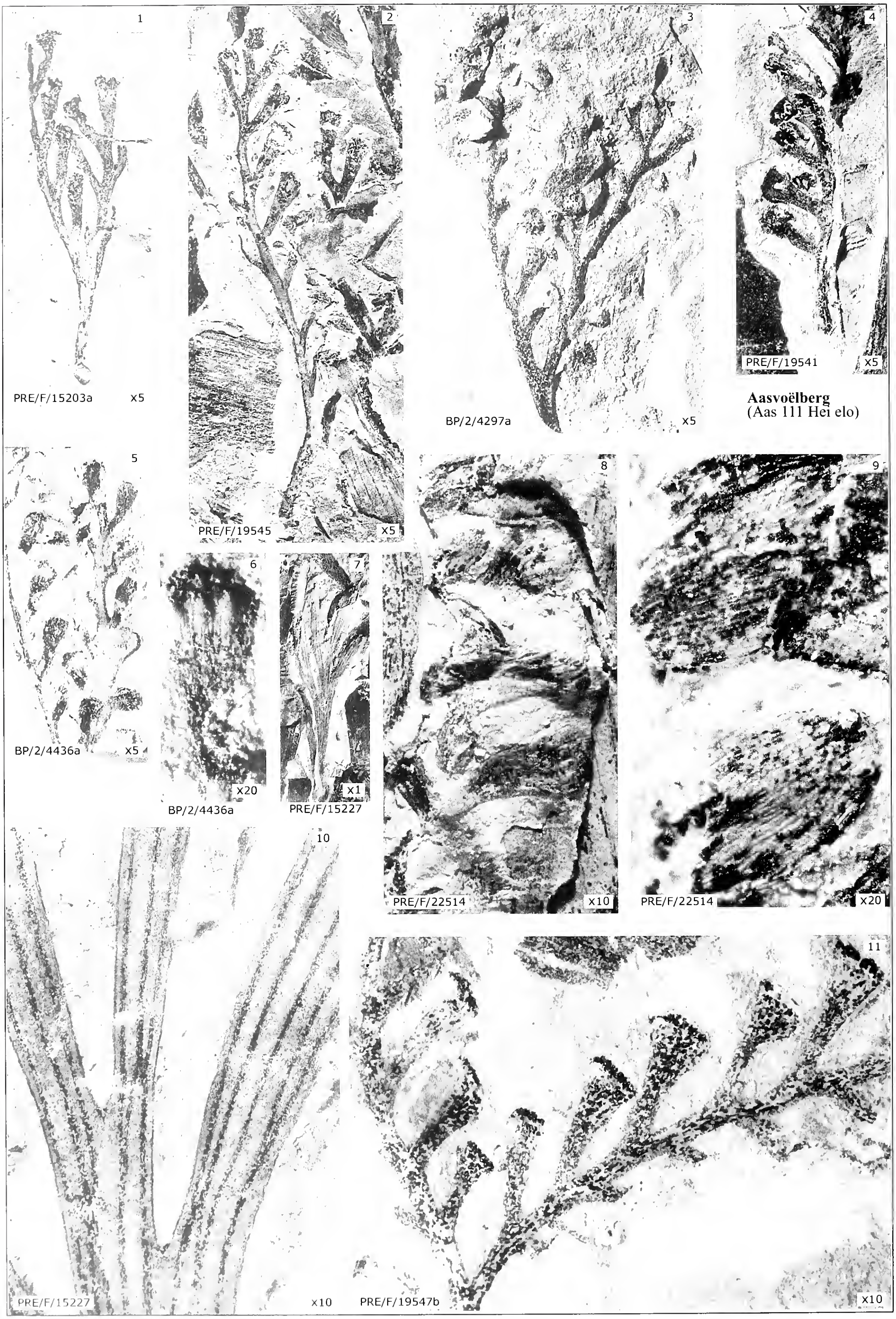
Kommandantskop
(Kom 111 Sph/Dic)



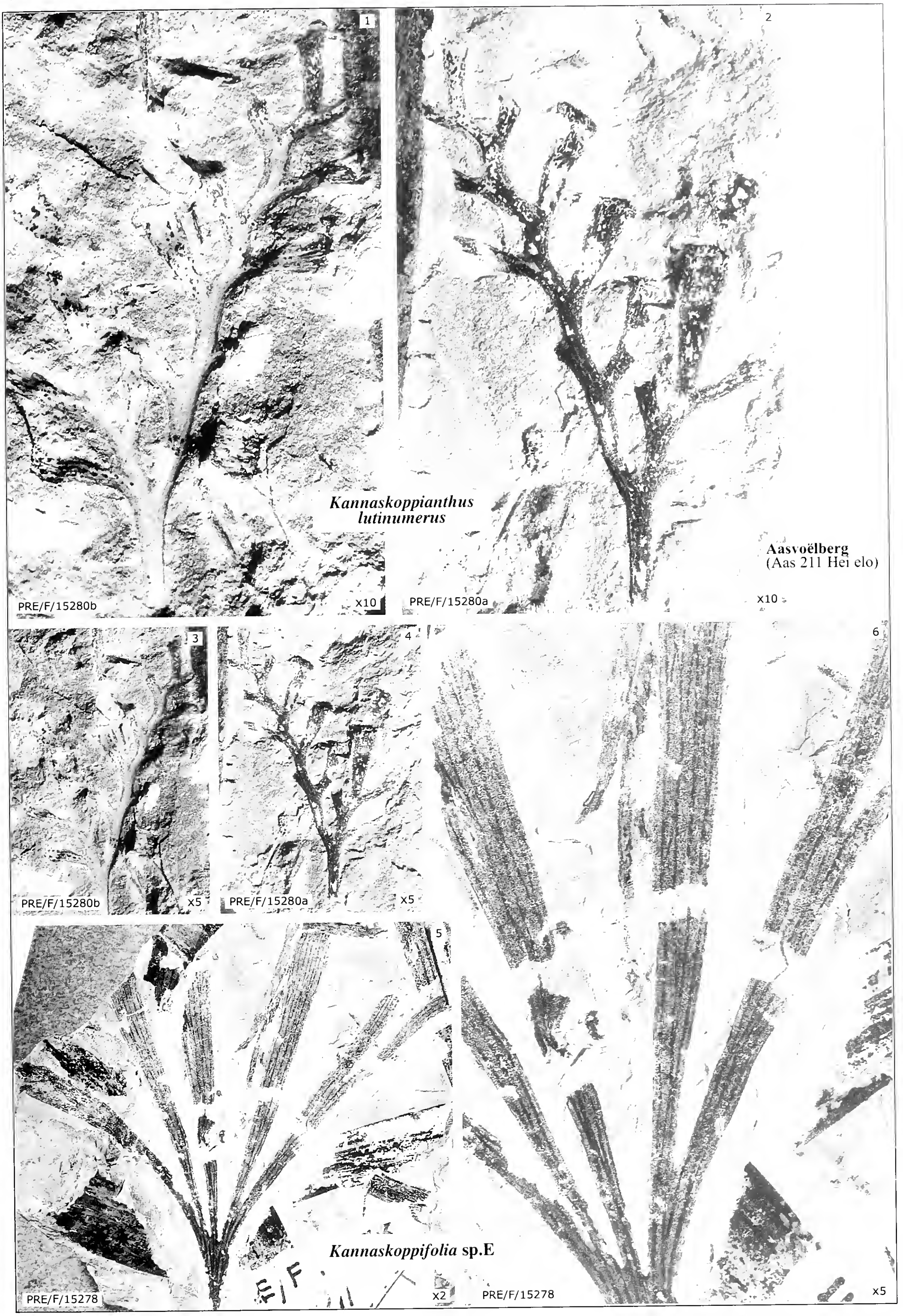
Kannaskoppianthus lutinumerus pl. 110 PETRIELLALES



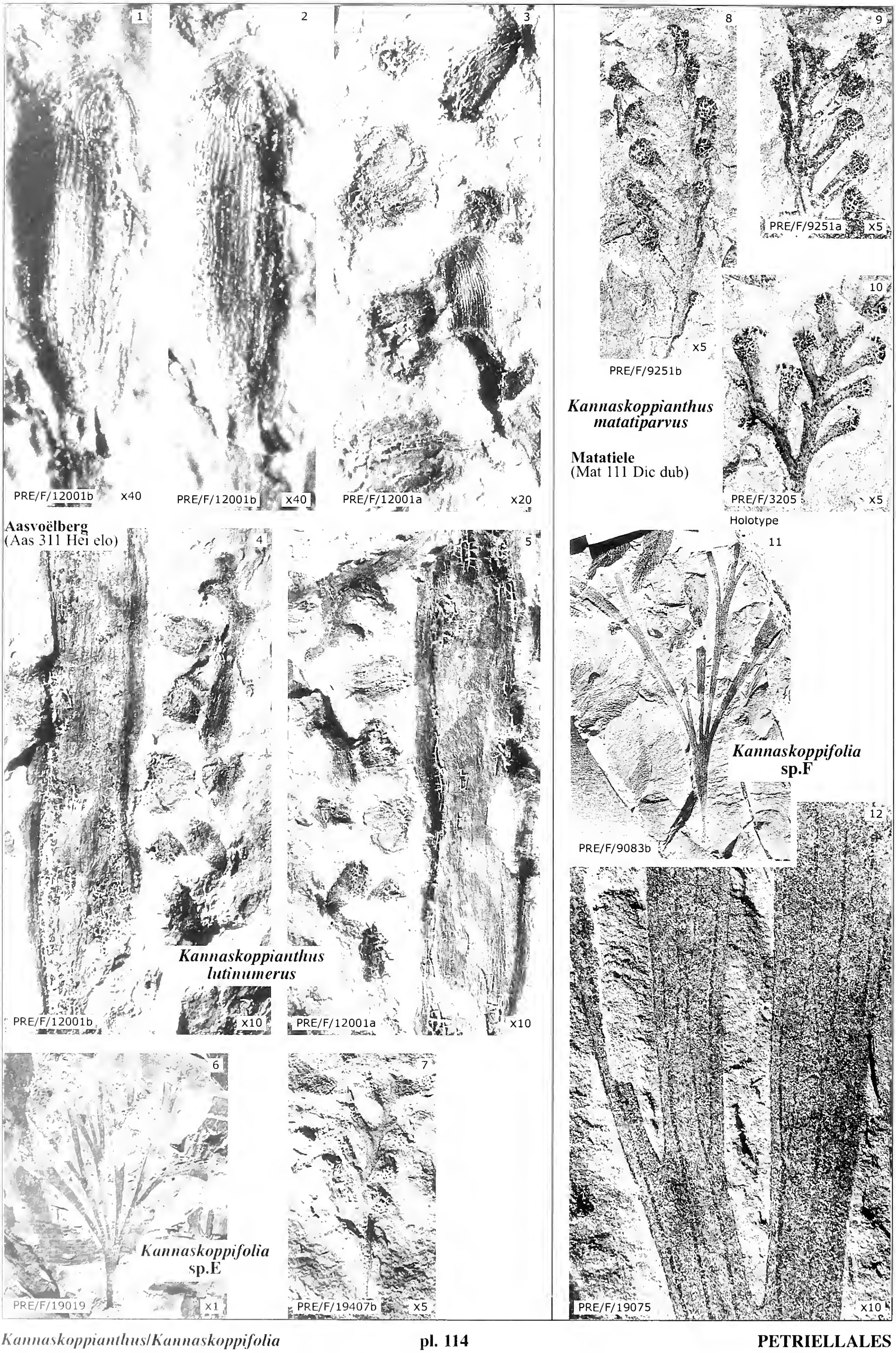
PETRIELLALES **pl. 111** ***Kannaskoppifolia* sp.D**

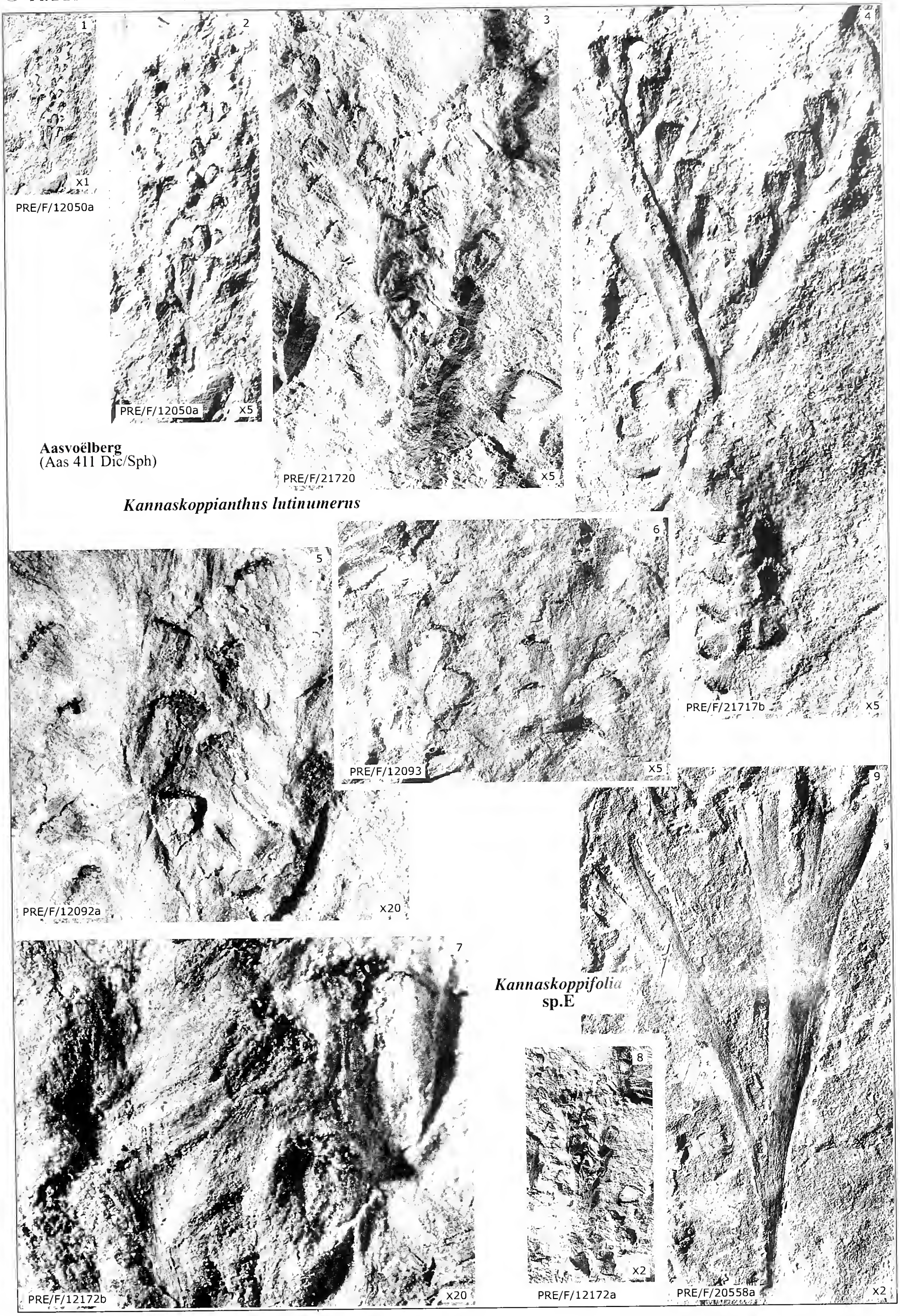


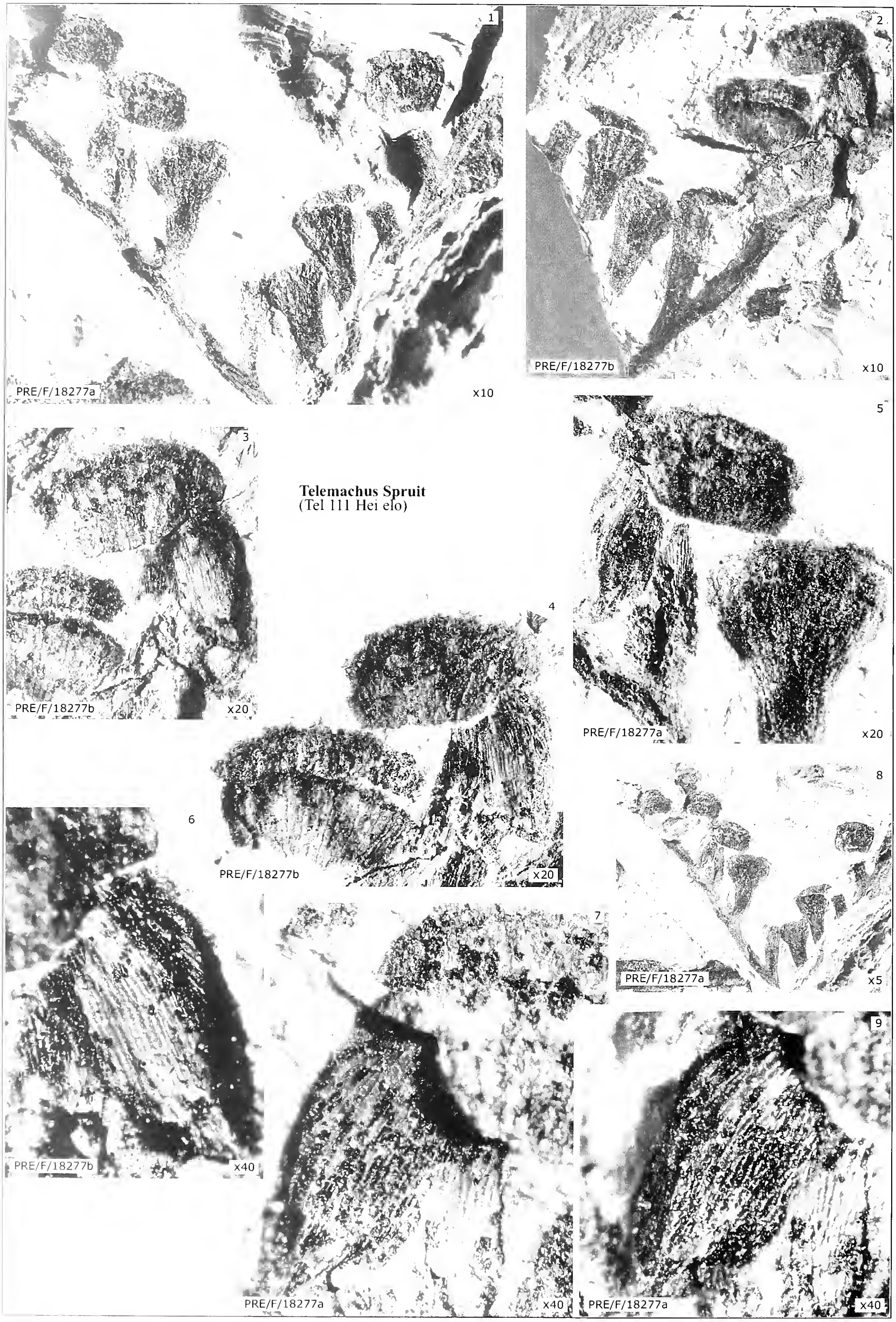
Kannaskoppianthus latinumerus **pl. 112** **PETRIELLALES**

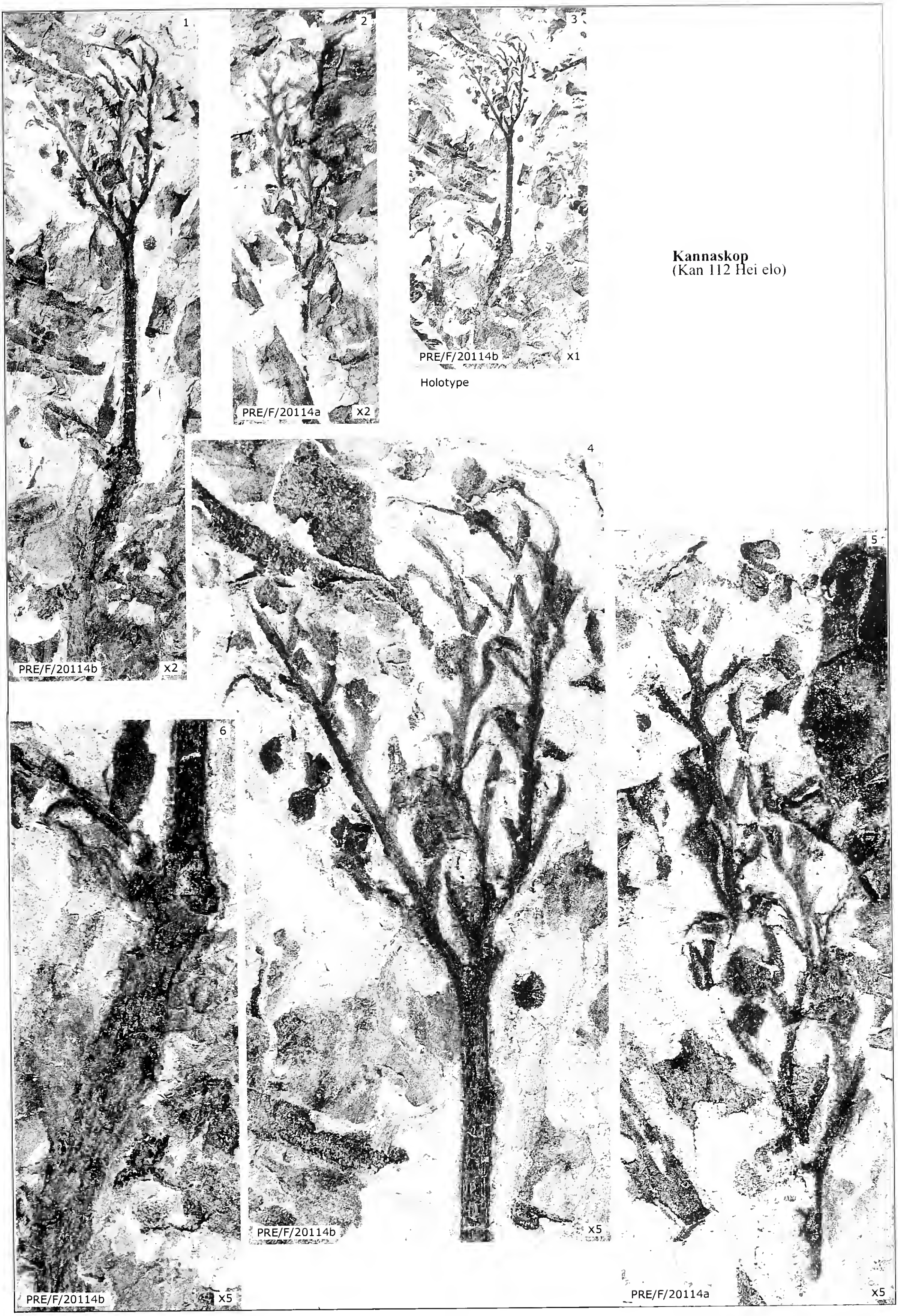


PETRIELLALES pl. 113 *Kannaskoppianthus/Kannaskoppifolia*


1
PRE/F/12001b x40
2
PRE/F/12001b x40
3
PRE/F/12001a x20
Aasvoëlberg
(Aas 311 Hei elo)
4
Kannaskoppianthus
lutinumerus
x10
PRE/F/12001b
5
PRE/F/12001a x10
6
Kannaskoppifolia
sp.E
PRE/F/19019 x1
7
PRE/F/19407b x5
8
x5
PRE/F/9251b
9
PRE/F/9251a x5
Kannaskoppianthus
matatiparvus
Matatiele
(Mat 111 Dic dub)
10
PRE/F/3205 x5
Holotype
11
Kannaskoppifolia
sp.F
PRE/F/9083b
12
PRE/F/19075 x10

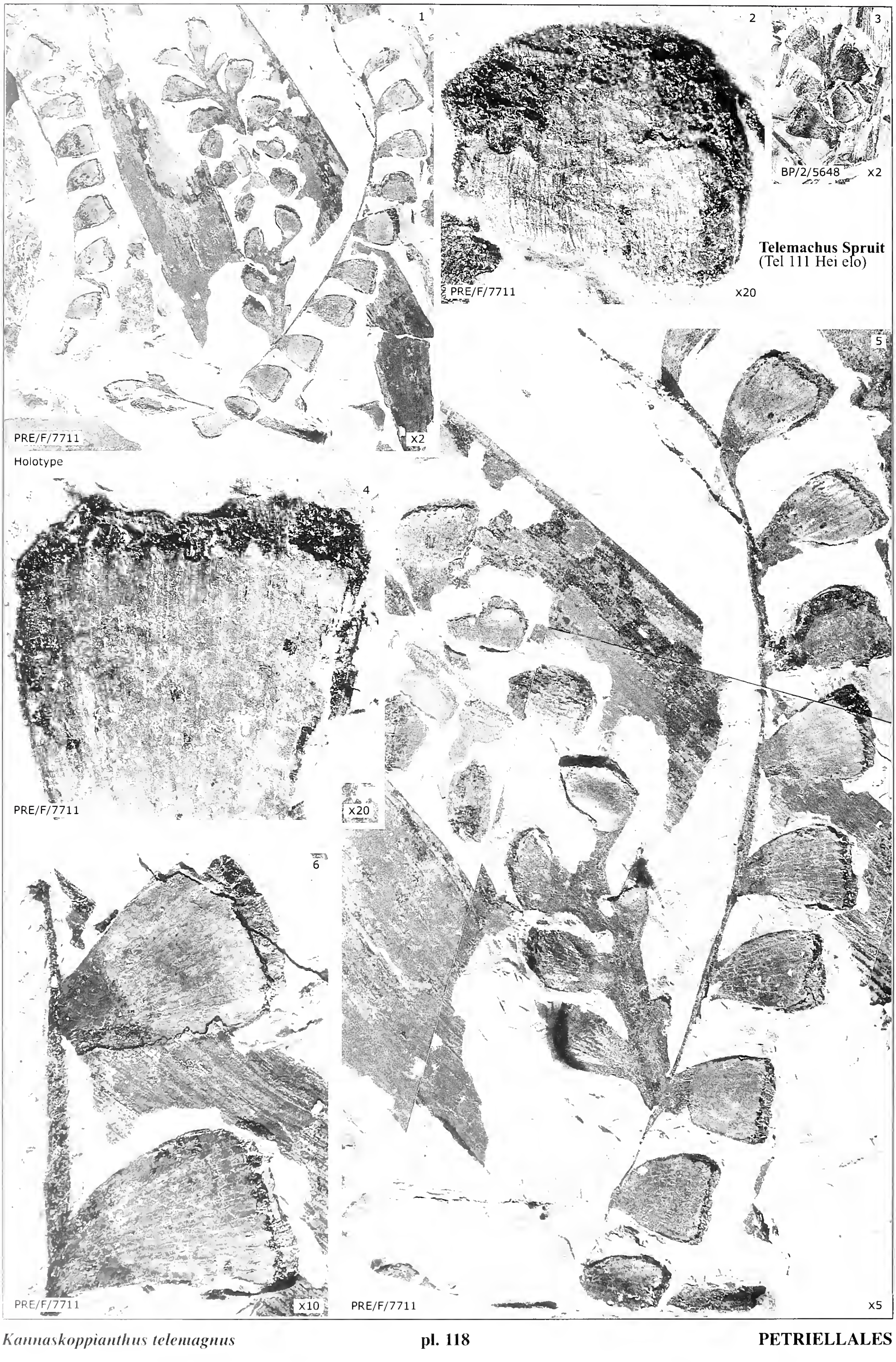

1
x1
PRE/F/12050a
2
PRE/F/12050a
x5
3
PRE/F/21720
x5
4
PRE/F/21717b
x5
Aasvoëlberg
(Aas 411 Dic/Sph)
Kannaskoppianthus lutinumerus
5
PRE/F/12092a
x20
6
PRE/F/12093
x5
7
PRE/F/12172b
x20
Kannaskoppifolia
sp.E
8
x2
PRE/F/12172a
9
PRE/F/20558a
x2


1
PRE/F/18277a
x10
2
PRE/F/18277b
x10
3
PRE/F/18277b
x20
Telemachus Spruit
(Tel 111 Hei elo)
4
PRE/F/18277b
x20
5
PRE/F/18277a
x20
6
PRE/F/18277b
x40
7
PRE/F/18277a
x40
8
PRE/F/18277a
x5
9
PRE/F/18277a
x40



Kannaskop
(Kan 112 Hei elo)

PETRIELLALES **pl. 117** ***Kannaskoppianthus irregularis***


1
2
3
BP/2/5648 x2
Telemachus Spruit
(Tel 111 Hei elo)
PRE/F/7711 x20
5
PRE/F/7711 x2
Holotype
4
PRE/F/7711
x20
6
PRE/F/7711 x10
PRE/F/7711
x5

PETRIELLALES **pl. 119** ***Kannaskoppifolia* sp.H**

GINKGOOPSIDA S.V.Meyen 1987
INCERTAE SEDIS order
INCERTAE SEDIS family

Cetifructus J.M.And. & H.M.And., gen. nov.

Type species
Cetifructus bilateralis J.M.And. & H.M.And., sp. nov.
Umkomaas Valley, Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis
A putative ginkgoopsid with a linear planar axis bearing opposite to subopposite pairs of simple sessile megasporophylls comprising a pack of several tiny linear-lanceolate ovules.

Generic characters
Strobilus: simple, small (up to *ca* 30 mm long), linear, laminate; axis flattened, with distinct midrib and flanges, strongly curved; megasporophylls opposite to subopposite, sessile, borne singly and semi-erect on truncate flattened flange projections.
Megasporophyll: apparently reduced to single small (*ca* 2 mm long), elliptical structures; ovules/seeds tightly packed, several per unit.
Ovule/seed: tiny (*ca* 2 x 0.2 mm), linear-lanceolate, striate.

Etymology
Cetifructus—cetus (Lat.), whale, with reference to the type locality Umkomaas (which means cow or whale in the local Zulu language); *fructus* (Lat.), fruit.

Global range: 1 sp., Gondwana, Tr. (CRN).
First & last: Molteno Fm.

Gondwana Triassic occurrence
SAf—Karoo Basin, 1 TC.

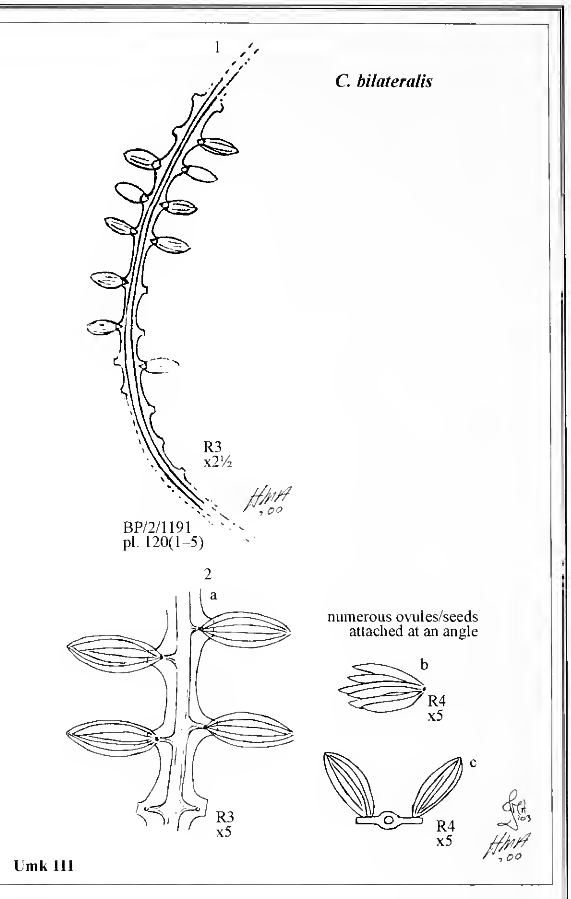
Molteno occurrence
Frequency (F): 1 TC (of 100 sampled in the Molteno).
Diversity (D): 1 species.
Abundance (A): 2 indivs.
Umk 111: 2 indivs in 400 man-hrs cleaving (1 per 20 man-days) extremely rare

With only two specimens from one TC, *Cetifructus* is one of the rarest of all Molteno fruit taxa. It does, however, meet our minimum criteria for inclusion as a newly named generic entity.

Affiliated organs
Male: unknown.
Foliage: unknown.

Classification & comparison
Suprageneric classification (family & order incertae sedis)
Cetifructus is unlike any other ovulate organ from the Molteno or known to us elsewhere in the fossil record. As the megasporophylls are possibly cupulate structures, we place the genus in the class Ginkgoopsida. However, owing to the uncertainty of the morphology, it is left in order and family incertae sedis.

Intergeneric comparison (Gondwana Triassic)
It is not impossible that *Cetifructus* is microsporangiate. The linear ovules/seeds, as interpreted, could in fact be pollen sacs. If so, and if our reconstructions (tfs 1, 2 adjacent) are correct, then there is a similarity between this genus and *Antevsia* (pp. 154, 155).



Reconstructions
With only two specimens at hand, the R3 and R4 reconstructions are tentative. Apart from the strobilus being planar with opposite to subopposite megasporophylls—features that are clear in the proximal(?) third of the holotype—the other illustrated and described characteristics are uncertain.

Strobilus
Though the simpler interpretation would be that the megasporophylls are attached distally and horizontally on the short stout projections, there are four pointers to the reconstruction preferred here: the apparent scars towards the centre of the flattened projections; the suggestion of vascular bundles leading to these scars but not beyond; the megasporangiate remnants at one of the points of attachment seeming to radiate outwards from a scar; and the megasporangia along one side of the holotype almost all being folded back across the axis.

Megasporophyll(?)
Whether these structures are compound as proposed—with a tight cluster of linear seeds partially or fully detached—or simple with one elliptical seed or cupule, is not certain. Since the material is extremely rare (1 specimen per 20 man-days cleaving), we have chosen not to macerate a specimen in the hope of resolving the uncertainties.

Cetifructus bilateralis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: BP/2/1191; pl. 120(1–5).
Assemblage: Umk111 Dic 2spp, Umkomaas Valley.
Preservation: incomplete strobilus without counterpart; compression in thinly laminated, carbonaceous (good cuticle) moderately baked, dark grey shale with good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 2 indivs (2 intact); pls 120(1–5), 121(1–5).

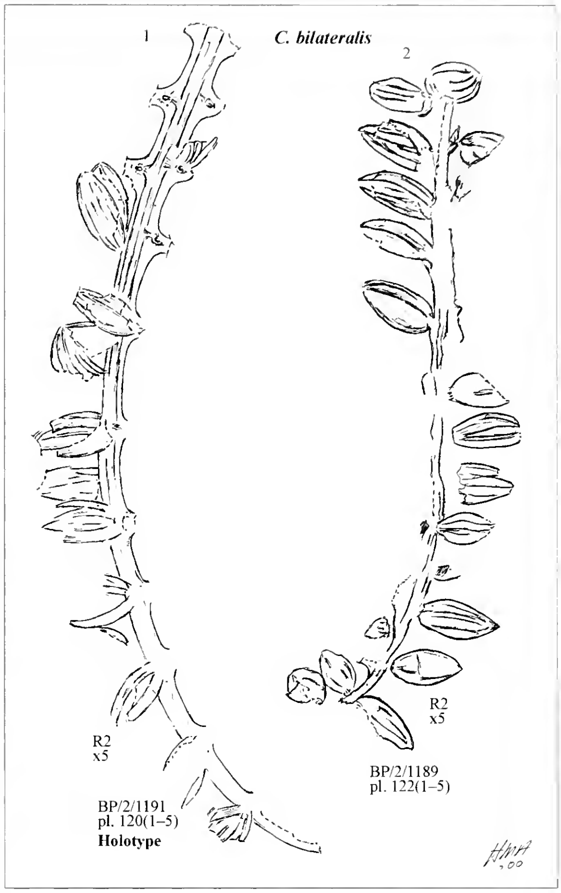
Sister palaeodemes—nil.

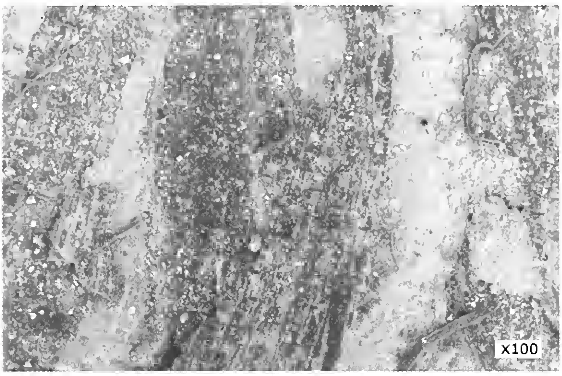
Specific diagnosis—as for genus.

Specific characters—as for genus.

Etymology
bilateralis—with reference to the two lateral rows of megasporangia.

Comment & comparison—see for genus.

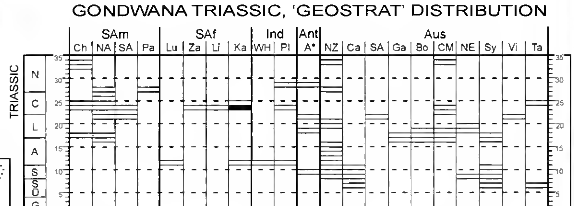


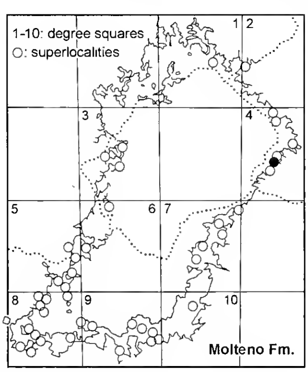


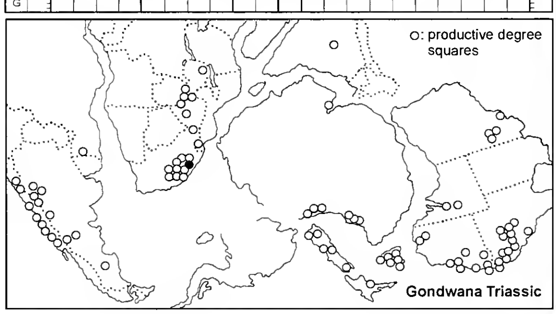
Umk 111 BP/2/1189

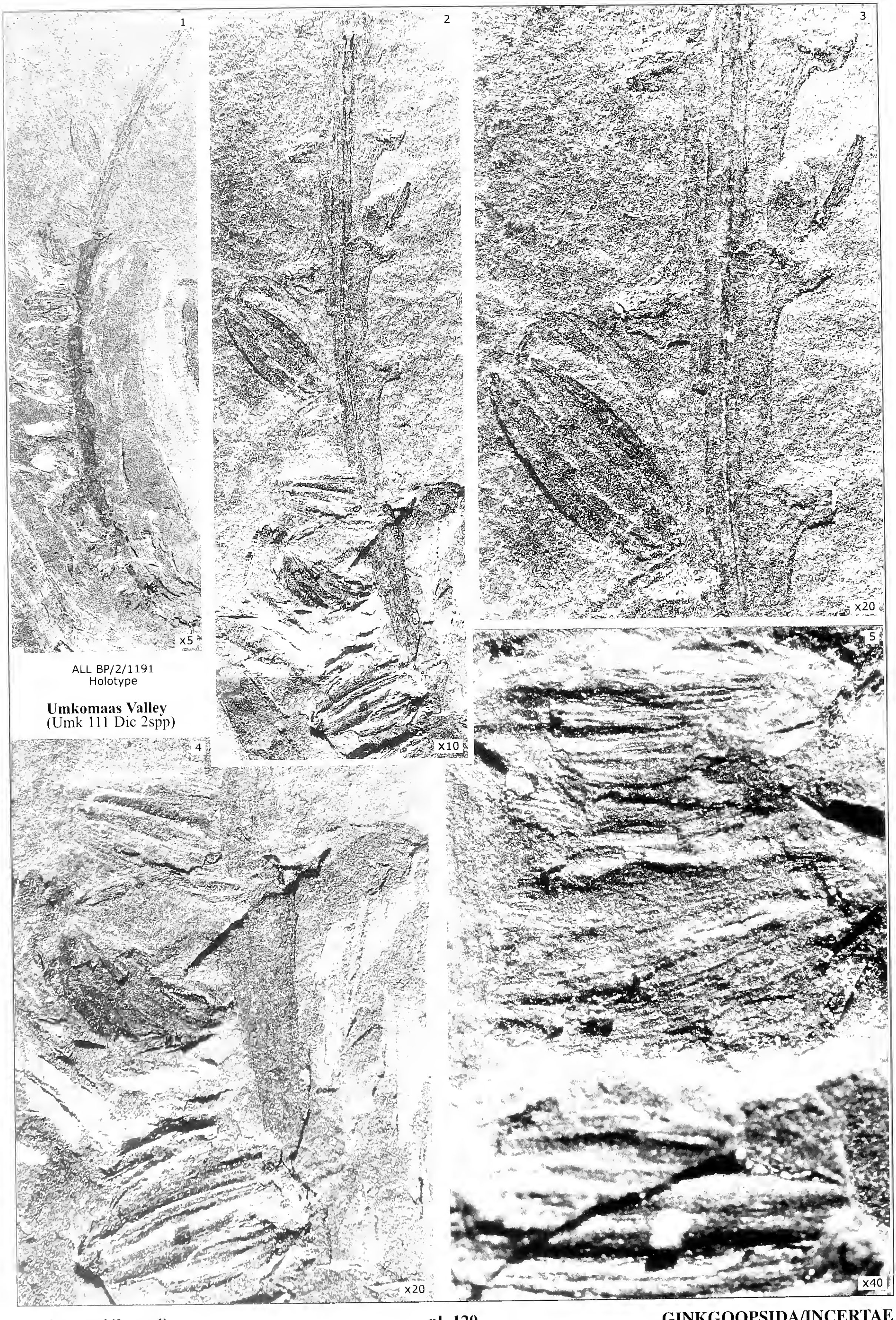
Cuticles
Potential sample: Umk 111, 2 indivs.
Macerated (this work): none.
Preservation grade: —
Diagnostic characters: —
Comment: In an attempt to obtain some information on the epidermal structure of *Cetifructus*, the material was placed under a Jed Scanning Microscope (5800 LV). Linear striations that are probably cell walls could be seen in certain places (see tfs 3, 4 adjacent) but no stomata or other structures were visible.
Significance: of no aid in classification and affiliation.

GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION



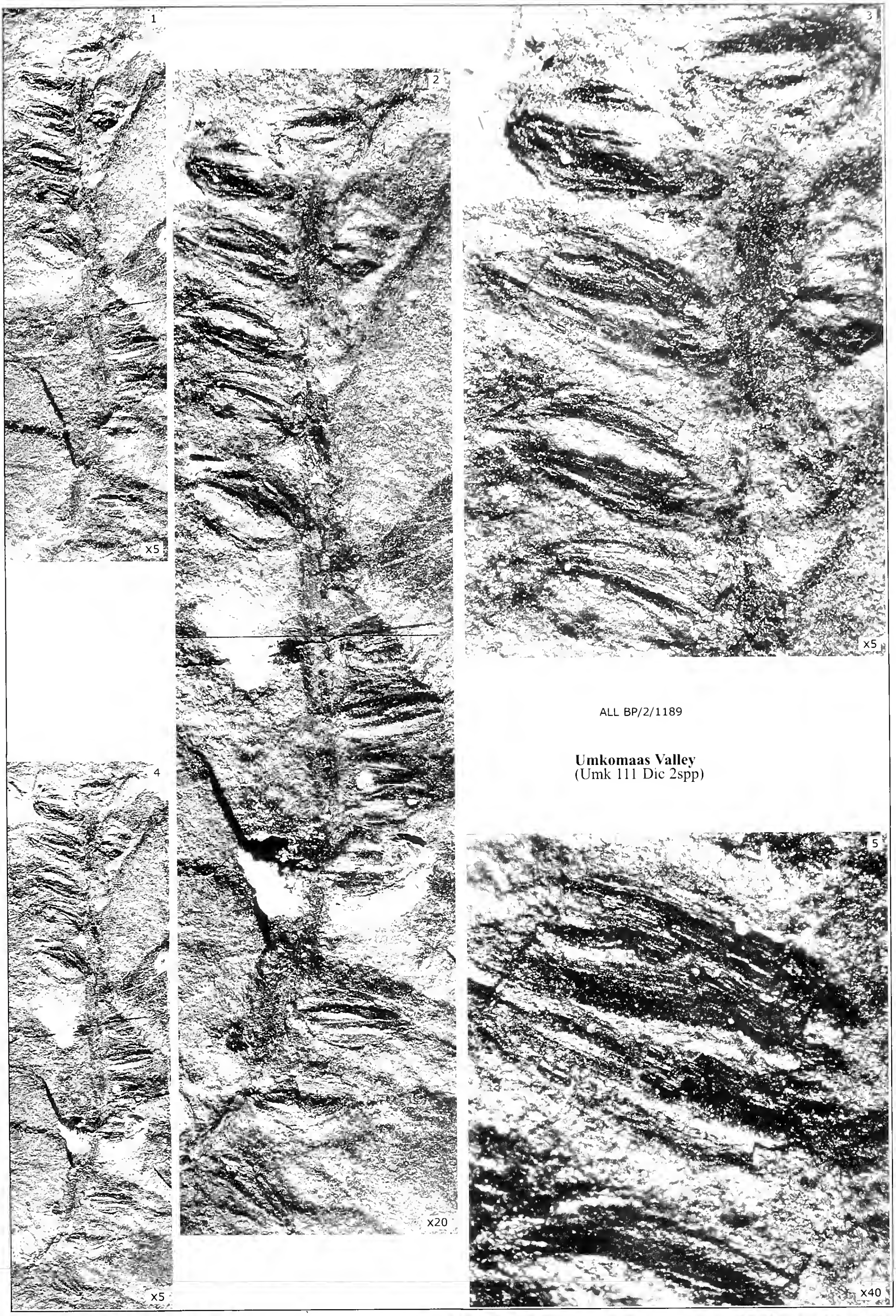






ALL BP/2/1191
Holotype

Umkomaas Valley
(Umk 111 Dic 2spp)



ALL BP/2/1189

Umkomaas Valley
(Umk 111 Dic 2spp)

INCERTAE SEDIS class

ALEXIALES J.M.And. & H.M.And., ord. nov.
ALEXIACEAE J.M.And. & H.M.And., fam. nov.

Alexia J.M.And. & H.M.And., gen. nov.

Type species
Alexia urceolus J.M.And. & H.M.And., sp. nov.
Umkomaas Valley, Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis
A putative gymnospermous ovulate strobilus of uncertain form, with linear planer axes bearing opposite rows of many simple sessile megasporophylls consisting of spherical pitcher-shaped cupules.

Generic characters
Strobilus: simple, small (>60 x *ca* 5 mm), linear planar 'catkin', gradually tapering; axis gracile, curved, free for >10 mm; megasporophylls numerous, sessile, opposite to alternate, decreasing gradually in size distally.
Megasporophyll: pitcher-shaped with funnel-like distal projection functioning as a stigmatic surface or micropyle; semiwoody rather than fleshy.
Ovule/seed: unknown; possibly single, completely enclosed and coinciding closely in dimension to the megasporophyll.

Eponymy
Alexia—in honour of Alex du Toit, the great pioneering geologist of South Africa and of continental drift, who made the first substantial collections from the Umkomaas locality (*ca* 1910–1917).

Global range: 1 sp., Gondwana, Tr. (CRN).
First & last: Molteno Fm.

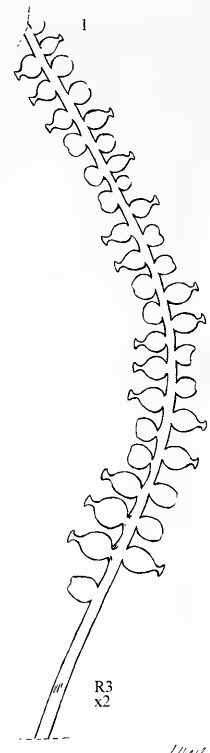
Gondwana Triassic occurrence
SAf—Karoo Basin, 1 TC (6 indivs).

Molteno occurrence
Frequency (F): 1 TC (of 100 sampled in the Molteno).
Diversity (D): 1 species.
Abundance (A): 6 indivs (1 strobilus, 5 isolated ovules).
Umk 111: 6 indivs in 400 man-hours (1 per *ca* 7 man-days) extremely rare

Affiliated organs: unknown.

Classification & comparison
Suprageneric classification (Alexiaceae/Alexiales)
A possible consideration is that *Alexia* is a fern belonging to a new advanced order with elaborately developed, pitcher-shaped indusia. The strobilus would then be regarded as a modified/reduced fertile frond—with the indusia attached directly to the midrib. However, the semiwoody aspect (rather than fleshy) and the fact that cuticle was obtained (fern cuticle being invariably delicate and difficult to isolate from Molteno fronds), point to this strobilus belonging to the Pinophyta (gymnosperms). Like several other new Molteno megasporangiate strobili, *Alexia* is unique and merits being placed in a new family (Alexiaceae) and order (Alexiales) and possibly even a new class (not named here).

Intergeneric comparison (Gondwana Triassic)
It is quite uncertain whether this single specimen represents the entire strobilus, or whether it is a detached megasporophyll. Our description assumes the latter. In this case there are some overall architectural similarities with *Hlatimbia*, which, however, we include in a separate unnamed class of fern-like gymnosperms.



Umk 111
PRE/F/18745a,b
pl. 122(1,2)

Reconstruction
Strobilus
Our reconstruction is based on the only strobilus available, specimen PRE/F/18745a,b, pl. 122(1), which is *ca* 60 mm long and incomplete. As the axis does not taper, its full length in life cannot be estimated. A distinct petiole is indicated by the absence of cupules towards the broken base. There is a slight decrease in size of the cupules distally. Isolated cupules are considerably larger than those attached to the axis. This, perhaps, is an indication of maturity or size range.

Cupules
The strobilus shows only one complete cupule, which is characterised by a pronounced funnel-like projection, pl. 122(4, 7, 8), and a second cupule with a partial projection. An isolated cupule shows a partially preserved funnel, pl. 123(1, 2). In the reconstruction (tf. 1 above) we show most cupules with the funnel-like projection.

Comparisons beyond Gondwana Triassic
A remote resemblance may be found in *Eophyllogonium*, a seed-bearing gigantopterid leaf from the Permian of China described by Mei *et al.* (1992). *Eophyllogonium* has a distinct leaf lamina with oval seeds attached along the margins. The single similarity is that both bear possible pollen traps, but the conical projections of *Eophyllogonium* are quite different from the funnel-shaped structures of *Alexia*.

A further resemblance occurs with the pitcher-shaped cupules of *Schmeissneria nicrostachys* (Kirchner & Van Konijnenburg-Van Cittert 1994) from the Liassic of Germany. However, the cupules of the Laurasian genus differ in being either sessile (if single) or pedunculate (when in pairs or more) and in bearing attached winged seeds. These strobili have been found in attachment with linear leaves (*cf. Glossphyllum* etc.) now also included in the genus *Schmeissneria* by the same authors.

Alexia urceolus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/18745a,b; pls 122(1–8), 123(7, 8).
Assemblage (TC): Umk 111 Dic 2spp, Umkomaas Valley.
Preservation: large section of strobilus, part and counterpart; compression in thinly laminated, carbonaceous (good cuticle), moderately baked, dark grey shale with good cleavage.

Reference palaeodeme
Assemblage (TC): as for the holotype.
Specimens: 6 indivs (1 intact, 5 isolated), pls 122, 123.

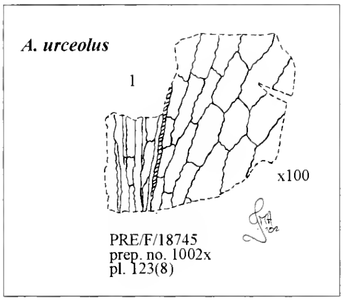
Sister palaeodemes—nil.

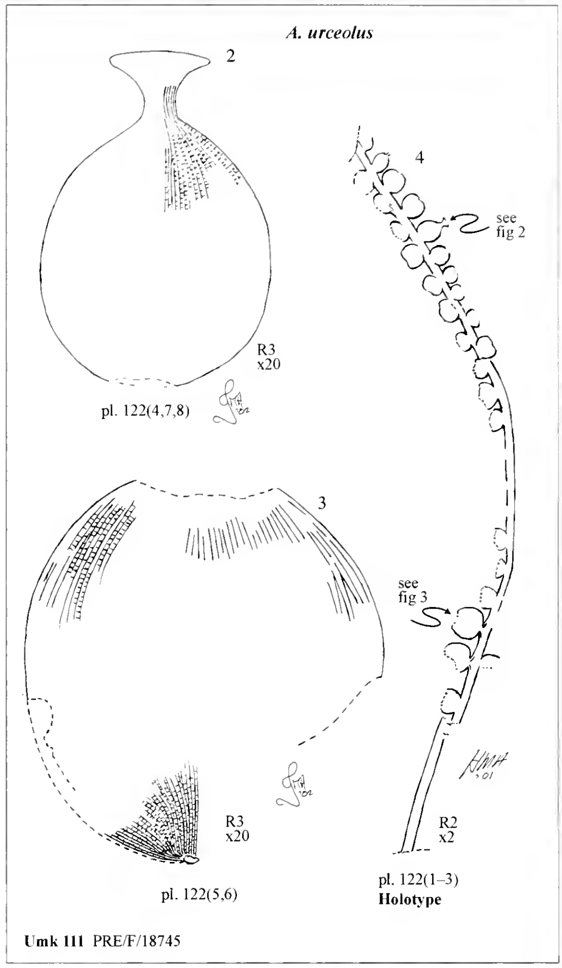
Specific diagnosis—as for genus.

Specific characters—as for genus.

Etymology
urceolus (Lat.)—a small jug or pitcher, with reference to the shape of the cupulate megasporophylls.

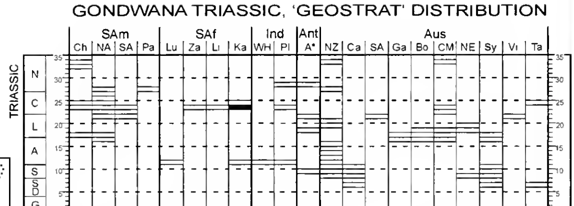
Comment & comparison—see for genus.

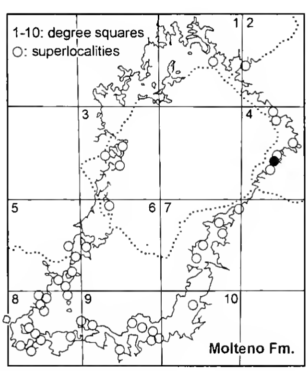


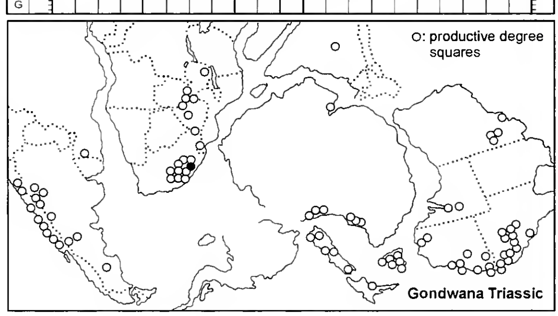


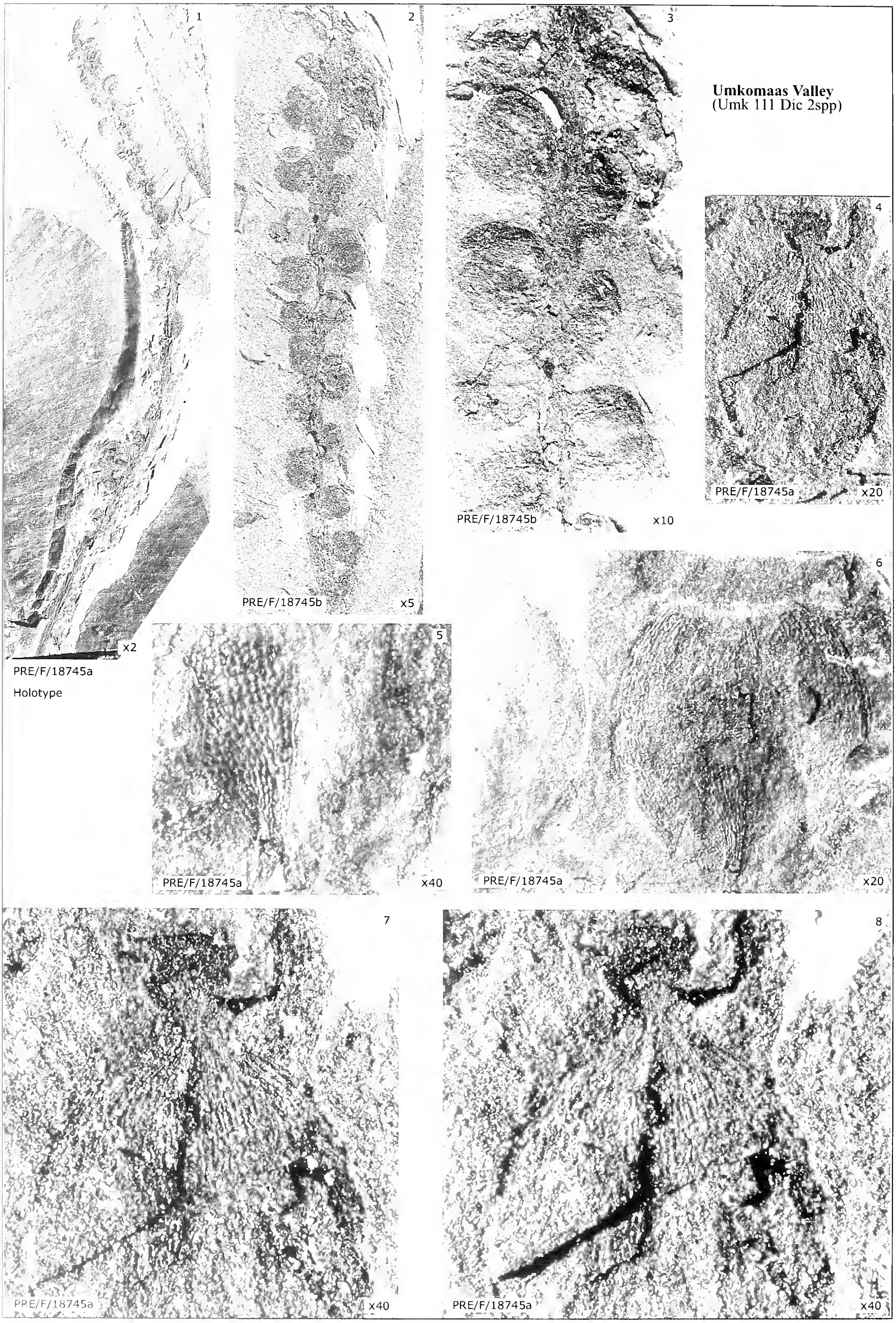
Cuticles
Potential sample: Umk 111, 6 indivs.
Macerated (this work): 1 indiv.
Preservation grade: Grade 3 (fair), cell outlines only, small pieces.
Diagnostic characters: cells oblong to linear, walls straight to gently curved to sinuous; other features absent.
Comment: —
Significance:
Classification—No cuticular features that aid in the classification of *Alexia* are available.
Affiliation—Remains unknown and the cuticle gives no further clues.

GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION

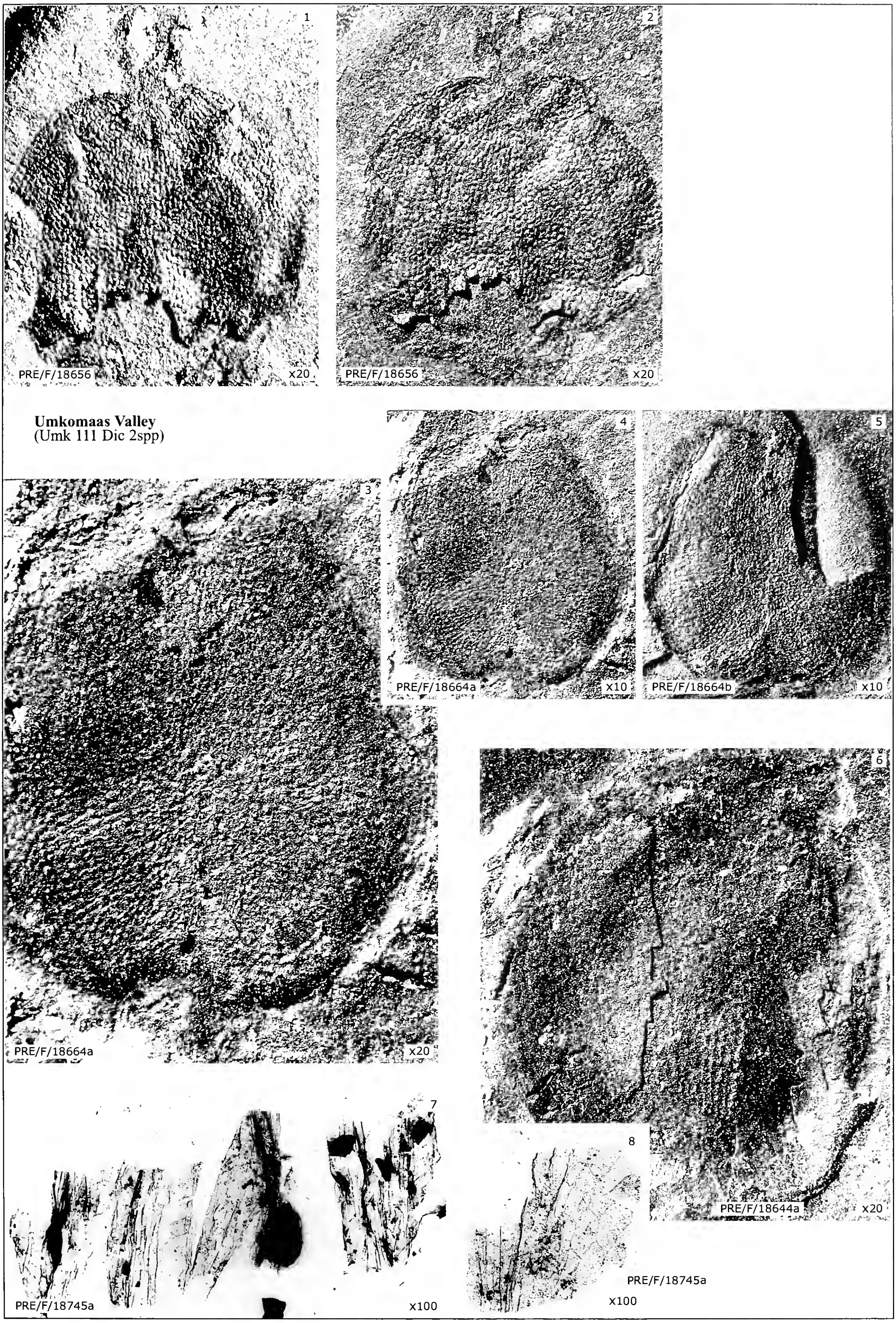








Alexia urceolus **pl. 122** **INCERTAE/INCERTAE**



INCERTAE/INCERTAE **pl. 123** ***Alexia urceolus***

INCERTAE SEDIS class
HLATIMBIALES J.M.And. & H.M.And., ord. nov.
HLATIMBIACEAE J.M.And. & H.M.And., fam. nov.

Hlatimbia J.M.And. & H.M.And., gen. nov.

Type species
Hlatimbia tommacleanii J.M.And. & H.M.And., sp. nov.
Hlatimbe Valley, Karoo Basin, S. Africa, Carnian, Triassic.

Generic diagnosis
A putative gymnospermous ovulate strobilus of planar pinnate form, with linear lateral axes bearing opposite rows of many simple pedunculate megasporophylls consisting of bivalved ovulate cupules.

Generic characters
Strobilus: compound, paniculate, relatively large (>200 x 65 mm), dorsiventral; main axis gracile (2–3 mm diam.); megasporophylls numerous, in opposite rows along linear planar secondary axis (*ca* 70 mm long), with a foliar tip.
Megasporophyll: simple, pedunculate; ovuliferous cupule bivalved (1.8 x 1.7 mm), bilaterally symmetrical; valves unequal, palmate, shallowly cupped, lower valve larger and more deeply and profusely lobed (up to 8 teeth) than the upper (up to 5 teeth).
Ovule: unknown.

Etymology
Hlatimbia—after the type locality Hlatimbe Valley.

Global range: 1 sp., Gondwana, Tr. (CRN).
First & last: Molteno Fm.

Gondwana Triassic occurrence
SAf—Karoo Basin, 1 TC.

Molteno occurrence
Frequency (F): 1 TC (of 100 sampled in the Molteno).
Diversity (D): 1 species.
Abundance (A): 2 indivs.

Hla 213: 2 indivs in 60 man-hours (1 per 3 man-days) very rare

Affiliated organs
Foliage: *Batiopteris pulchella*—Grade 2 (Mut. occ.).
Male strobilus: unknown.

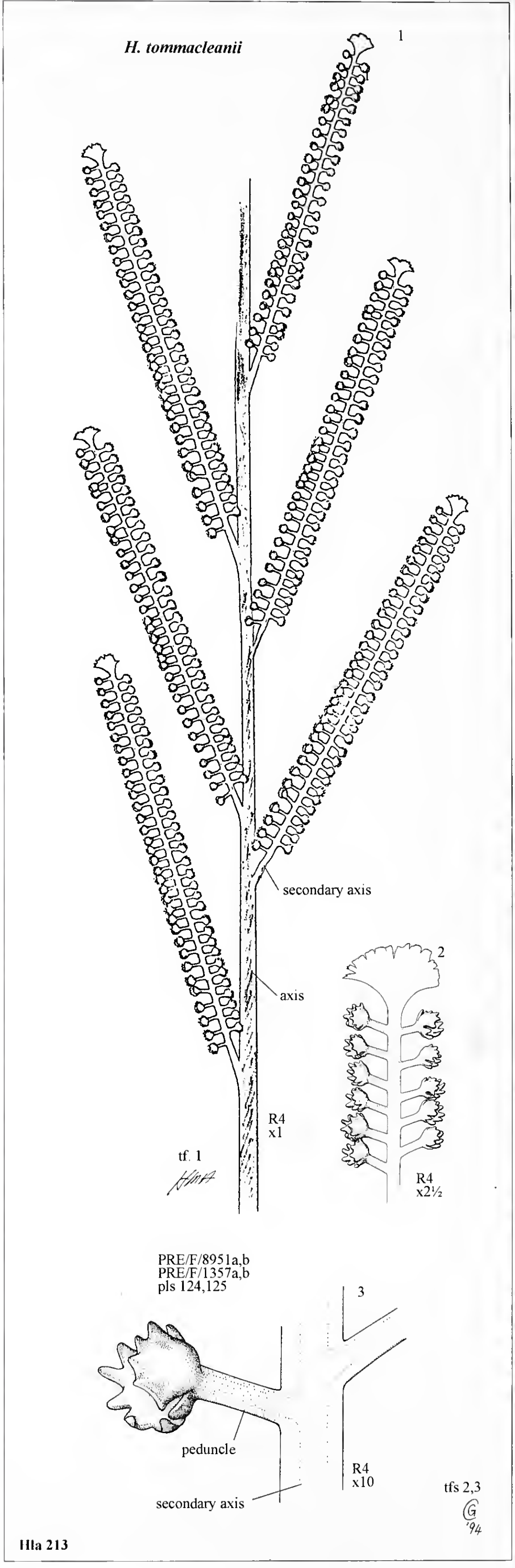
A unique foliar tip is preserved on one of the lateral axes (tf. 2 adjacent) of *Hlatimbia*. This shows a similar shape to *Batiopteris* leaves from the same TC and hence our Grade 2 affiliation.

Classification & comparison
Suprageneric classification (Hlatimbiaceae/Hlatimbiales)

At first glance, *Hlatimbia* gives the impression of being a rather bizarre form of fertile fern frond, but the bivalved cupules and the absence of sori place the genus in the Pinophyta (gymnosperms). We regard *Hlatimbia* as most likely an ovulate structure—neither ovules or pollen are known—and place it in the class incertae sedis. The unique bivalved cupules and general architecture of the strobilus merit placing it in the new order Hlatimbiales and family Hlatimbiaceae.

Intergeneric comparison (Gondwana Triassic)

The nearest Molteno ovulate genus to *Hlatimbia* appears to be *Alexia*, which, however, is sufficiently remote as to suggest a separate unnamed class of fern-like gymnosperms.



Hlatimbia tommacleanii J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/8951a,b,c; pls 124(1–7), 125(7, 8).
Assemblage (TC): Hla 213 Dic elo, Hlatimbe Valley.
Preservation: large portion of an incomplete strobilus, part and counterpart; compression in thinly laminated, carbonaceous (poor cuticle), medium dark grey shale with good cleavage.

Reference palaeodeme
Assemblage: as for holotype.
Specimens: 2 individuals; both fairly substantial portions of strobilus.

Sister palaeodemes—nil.

Specific diagnosis—as for genus.

Specific characters—as for genus.

Eponymy
tommacleanii—in memory of Tom Maclean, on whose farm the Hla 213 site occurs.

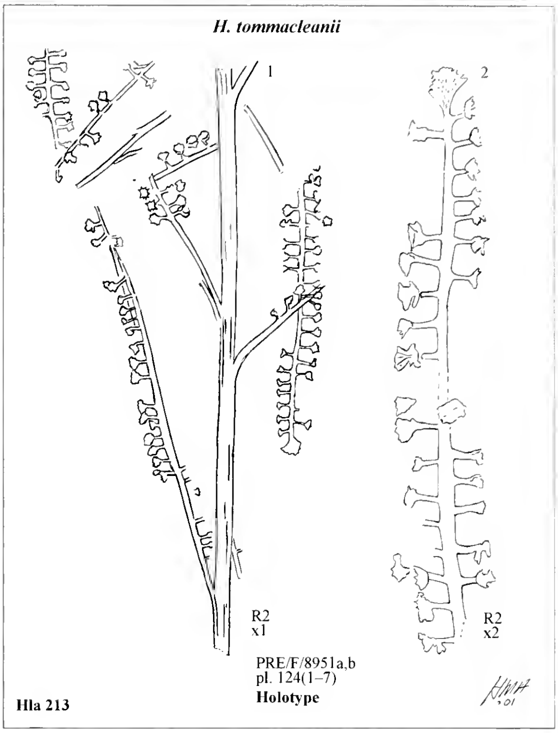
Classification & comparison—see for genus.

Reconstruction
Strobilus
This remarkable paniculate strobilus is shown in the reconstruction opposite, tf. 1. The main axis in PRE/F/8951a (tf. 1 adjacent) shows four lateral axes attached and further broken fragments to the upper left, possibly indicating another two detached lateral axes. The R4 reconstruction shows a basally and apically incomplete main axis bearing six lateral axes.

In the second specimen, PRE/F/1357, one lateral axis is clearly attached and fragments of a further six detached lateral axes are also present. The two specimens possibly belong to the same strobilus, but owing to missing matrix, the fossiliferous slabs do not fit together. Should the two specimens belong together, then the strobilus would have at least 11 lateral axes and be *ca* 250 mm long.

Foliar tip
The curious foliar tip is seen only on one lateral axis on specimen PRE/F/8951a, pls 124(1–3), 125(7, 8). We assume that in life the foliar tip would occur on all lateral axes, as in the reconstruction.

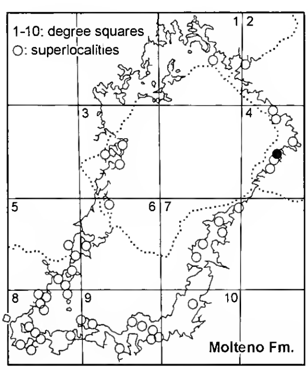
Megasporophyll/cupule
The bivalved cupule structure has been determined by excavation into the matrix and observing that the valves lie at two levels. Usually only one side is readily visible, but many of the cupules are variously flattened and show portions of both upper and lower valves, pl. 124(3, 4). The distal lobes vary from the usual simple projections, pl. 124(5–7), to the more rare bilobed projections, pl. 125(9).

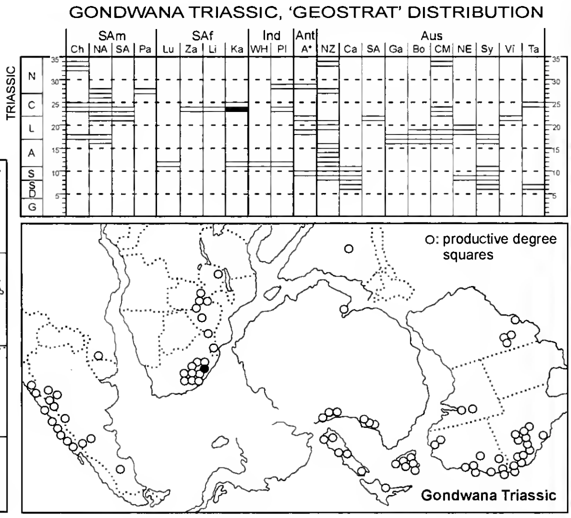


Classification beyond Gondwana Triassic
Laurasia Triassic
There is some similarity to the male strobilus *Ixostrobus* described by Schweitzer (1977) from the Alborz Mountains, Rhaetic of Iran (see also Harris & Miller 1974). *Ixostrobus* has four pollen sacs which are united to form a woody cup-shaped synangium. It is not impossible that *Hlatimbia* could be a male strobilus. Even so, it is still very different from *Ixostrobus* which has a spiral arrangement of synangia along the axis.

Other ages
The bivalved cupules of *Hlatimbia* show some resemblance to *Leptostrobus* from the Yorkshire Jurassic of England (see *L. cancer*, Harris & Miller 1974). The latter genus has cupules with an upper and lower valve, but it differs in all other respects, such as the attachment to the axis, the presence of seeds and the smooth margin of the cupule.

Both *Ixostrobus* and *Leptostrobus* have clear affiliation to *Czekanowskia* leaves (unknown from the Molteno) and are placed in the order Leptostrobales.





Batiopteris J.M.And. & H.M.And., gen. nov.

Type species
Batiopteris pulchella J.M.And. & H.M.And., sp. nov.
Hlatimbe Valley, Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis
A gymnospermous leaf of uncertain class with long gracile petiole and fan-shaped bifidly dividing lamina with frequently anastomosing venation.

Generic characters
Attachment: unknown.
Leaf: fan-shaped, broadly cuneate to conspicuously auriculate; lamina entire to deeply and serially bifidly divided; petiole distinct, long, gracile; venation frequently anastomosing, forming an open mesh.
Cuticle: this vol., see opposite.

Etymology
Batiopteris—batia (Gr.), bush, with reference to Hlatimbe based on the Zulu word for bush; *pteris* (Gr.), fern.

Global range: 7 spp., Gondwana, Tr. (LAD–CRN).
First: *Batiopteris* (*Chiropteris barrealensis*) (Frenguelli 1942); Barreal Fm., Quebrada de la Cortaderita, Barreal, N. Argentina.
Last: *Batiopteris zeilleri*, Molteno Fm.

Gondwana Triassic occurrence
Frequency (F): 7 degree squares (of the 84 across Gondwana).
Ubiquity (U): 3 continents (of 5 comprising Gondwana).
Diversity (D): 7 species.
Abundance (A): <1% (as recorded for the Molteno).
Longevity (L): 2 myrs (Lower Carnian).
Colonisation success: FUDAL rating 7/3/7/–/2 = 19.
Limited success (Grade 2); *Batiopteris* was the 18th most prominent genus in the Gondwana Triassic; it was relatively ubiquitous and diverse, but was infrequent, everywhere rare, and of apparently very short longevity.
Endemism: In the thinly scattered nature of the palaeodemes and the rarity of specimens, endemism was characteristically high in *Batiopteris*. Four of the five Molteno species are single-assemblage endemics.

Molteno occurrence
Frequency (F): 10 TCs (of 100 sampled in the Molteno).
Diversity (D): 5 species.
Abundance (A): occasional (2%) in 1 TC; vanishingly rare (<1%) in 9 TCs.
Habit: possibly a slender, twining, herbaceous climber.
Preferred habitat: each species occurred in a different habitat, from riparian forest to *Heidiphyllum* thicket and fern meadow.

Affiliated organs
Female strobilus: *Hlatimbia*—Grade 2 (Mor. occ.).
Male strobilus: unknown.

Classification & comparison
Suprageneric classification
Batiopteris pulchella, and its affiliated megasporophyll *Hlatimbia*, are tentatively placed in a new order and family.

Intergeneric comparison
Chiropteris, originally described from the Triassic in Germany, is a heterogenous group of leaves (Retallack 1980a) with anastomosing venation and similar leaf shape to *Batiopteris*. However, *Batiopteris* is regarded as distinct in view of affiliation with *Hlatimbia* and occurrence in Gondwana.

Gontriglossa, *Cetiglossa*, *Gracilliglossa* and *Kannaskoppifolia* all have anastomosing venation but differ from *Batiopteris* in the form of venation and lamina shape. Some species of *Ginkgoites* are similar to *Batiopteris* in leaf shape but differ by the lack of anastomoses in the venation.

Additional Molteno leaves here listed as *Batiopteris* sp.A to sp.C will be formally described in a future publication.

Gondwana Triassic occurrence (elaborated)
Batiopteris occurs very infrequently and rarely in South Africa and elsewhere in Gondwana Triassic floras. Many leaves previously placed in *Chiropteris* can now be included in *Kannaskoppifolia* or *Rochipteris* Herbst *et al.* 2001. Those now regarded as *Batiopteris* are:

South America (N. Argentina)
1942 Frenguelli: *Chiropteris barrealensis*, tf. 1, 2, pl. 1, 2(1, 2); a species based on four illustrated specimens; one 'locality' (Quebrada de la Cortaderita), Barreal-Hillario Basin, Barreal Fm., L. Carnian, U. Triassic.
1963 Bonetti (unpubl. thesis): *Chiropteris barrealensis*, pls 8(1, 2), 10(1, 2), 32(6–8); seven illustrated individuals; one 'locality' (Punto 11), Barreal-Hillaria Basin, Barreal Fm.

Australia (Tasmania)
1888 Johnston: *Sagenopteris salisburioides*, f. 28 (4, 4A); a species based on two very poorly illustrated individuals; one locality (Lords Hill), Hobart, Brady Fm. equivalent, Carnian, U. Triassic.

South Africa (Karoo Basin)
1903 Seward: *Chiropteris zeilleri*, tf. 7; a species based on a single specimen from Cyphergat, Molteno Fm. (illustrated here, tf. 5, opposite).

Batiopteris pulchella J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/8697a,b; pls 126(16, 29), 127(3).
Assemblage (TC): Hla 213 Dic elo, Hlatimbe Valley.
Preservation: complete leaf, part and counterpart; compression in thinly laminated, carbonaceous (poor cuticle) medium dark grey shale with good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 43 indivs.

Sister palaeodemes—nil.

Specific diagnosis
A *Batiopteris* leaf of small size with distinct petiole, moderately auriculate proximal lamina margin and variously divided distal lamina margin.

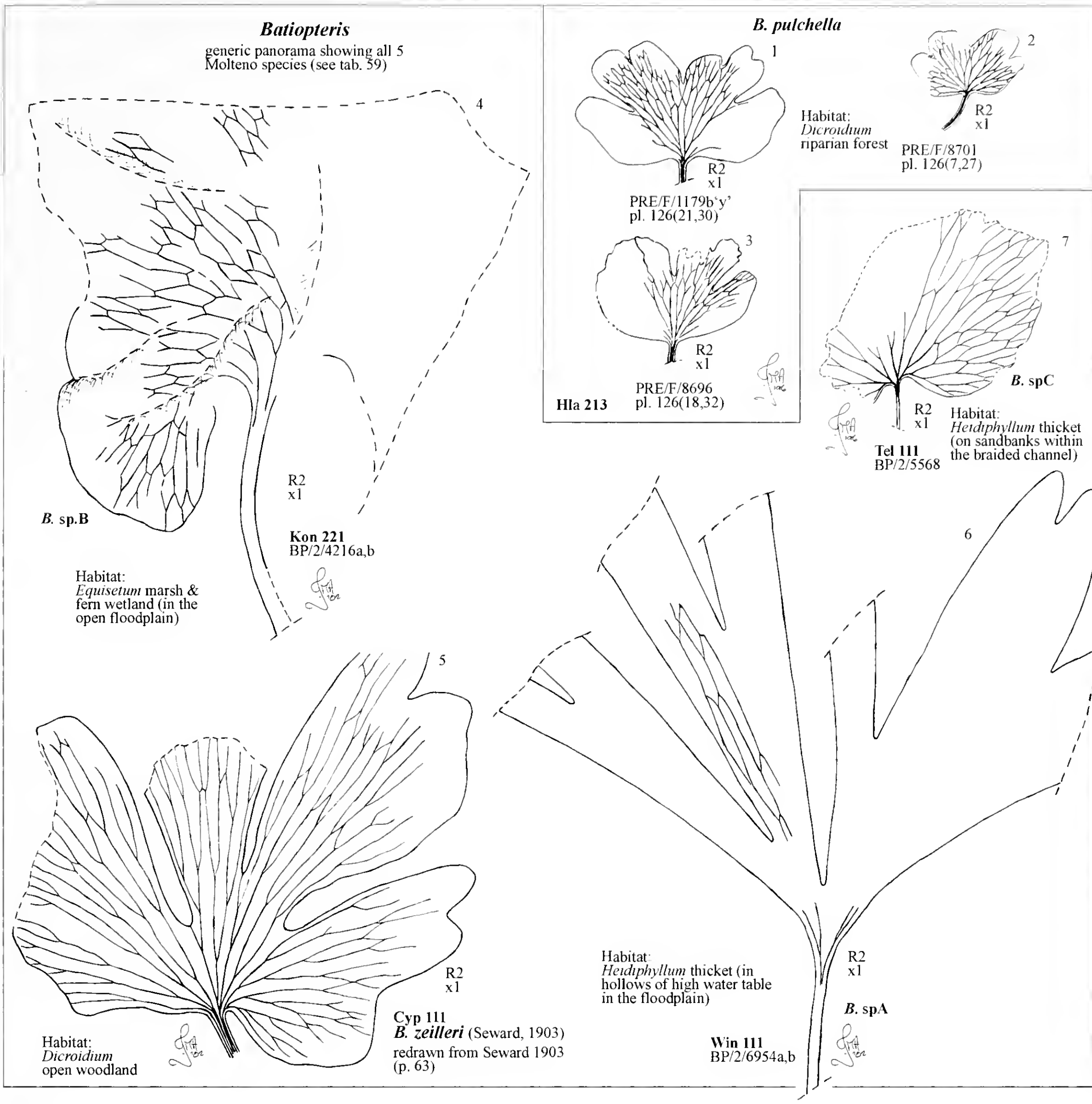
Specific characters
Leaf: small, *ca* 0.5–20 mm long and 0.5–30 mm wide; petiole distinct, *ca* 0.6 mm long and 0.5–1.0 mm wide; lamina variously divided (in smaller leaves once, in larger leaves up to 4 times), lobes obtuse; veins in larger leaves *ca* 1 mm apart, with forks and anastomoses at *ca* 0.5–0.8 mm intervals.

Etymology
pulchella (Lat.)—beautiful, with reference to the attractive leaves.

Comment & comparison
This species differs from other *Batiopteris* species in the combination of size, shape and venation.

assemblages (taphocoenosis)		*Batiopteris*	*B. pulchella* (Hla 213)	" *zeilleri* (Cyp 111)	" sp.A (Win 111)	" sp.B (Kon 221)	" sp.C (Tel 111)	" *spp. indet.*	♀ *Hlatimbia*
Bir 111	Sph 2spp	1	-	-	-	-	-	1	-
Cyp 111	Dic cra	20	-	20	-	-	-	-	-
Tel 111	Hei elo	1	-	-	-	-	1	-	-
Kon 223	Dic odo	1	-	-	-	-	-	1	-
Kon 221	Ast 2spp	2	-	-	-	2	-	-	-
Kon 211	Ast 2spp	6	-	-	-	6	-	-	-
Win 111	Hei elo	1	-	-	1	-	-	-	-
Hla 213	Dic elo	**2**	**2**	-	-	-	-	-	2
Umk 111	Dic 2spp	2	-	-	-	-	-	2	-
Aas 311	Hei elo	1	-	-	-	-	-	1	-
Total TCs		10	1	1	1	2	1	4	1
Total indivs		%	%	20	1	8	1	5	2

Tab. 59. ***Batiopteris*, Molteno occurrence**



Cuticles

Potential sample: Umk 111, 2 indivs; Hla 213, 43 indivs.

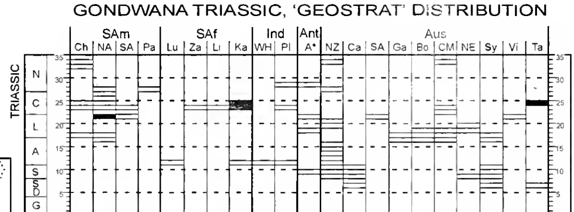
Macerated (this work): Umk 111, 2 indivs.

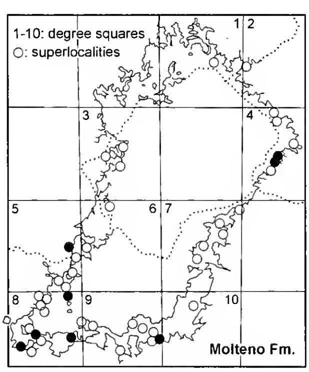
Preservation grade: Grade 2.

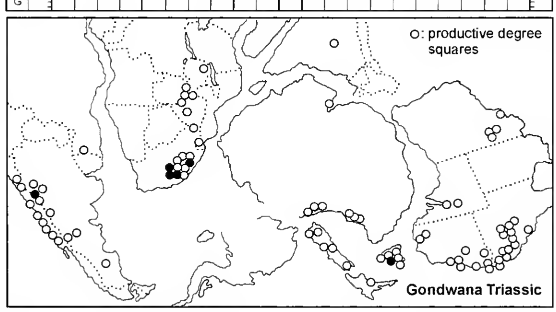
Diagnostic characters: cell structure present, but without diagnostic features.

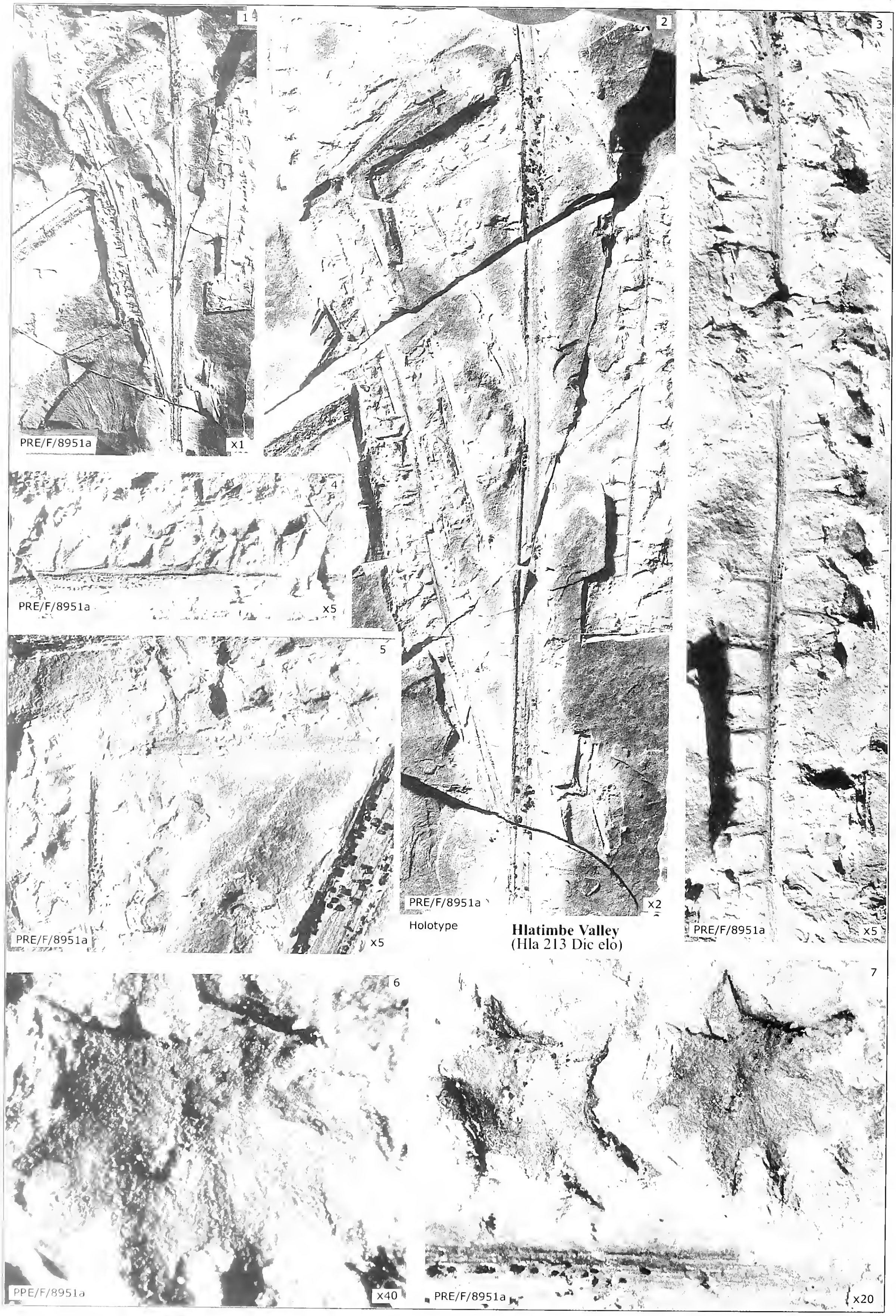
Comment: minimal interpretable structure obtained.

Significance: of no value in classification or affiliation.





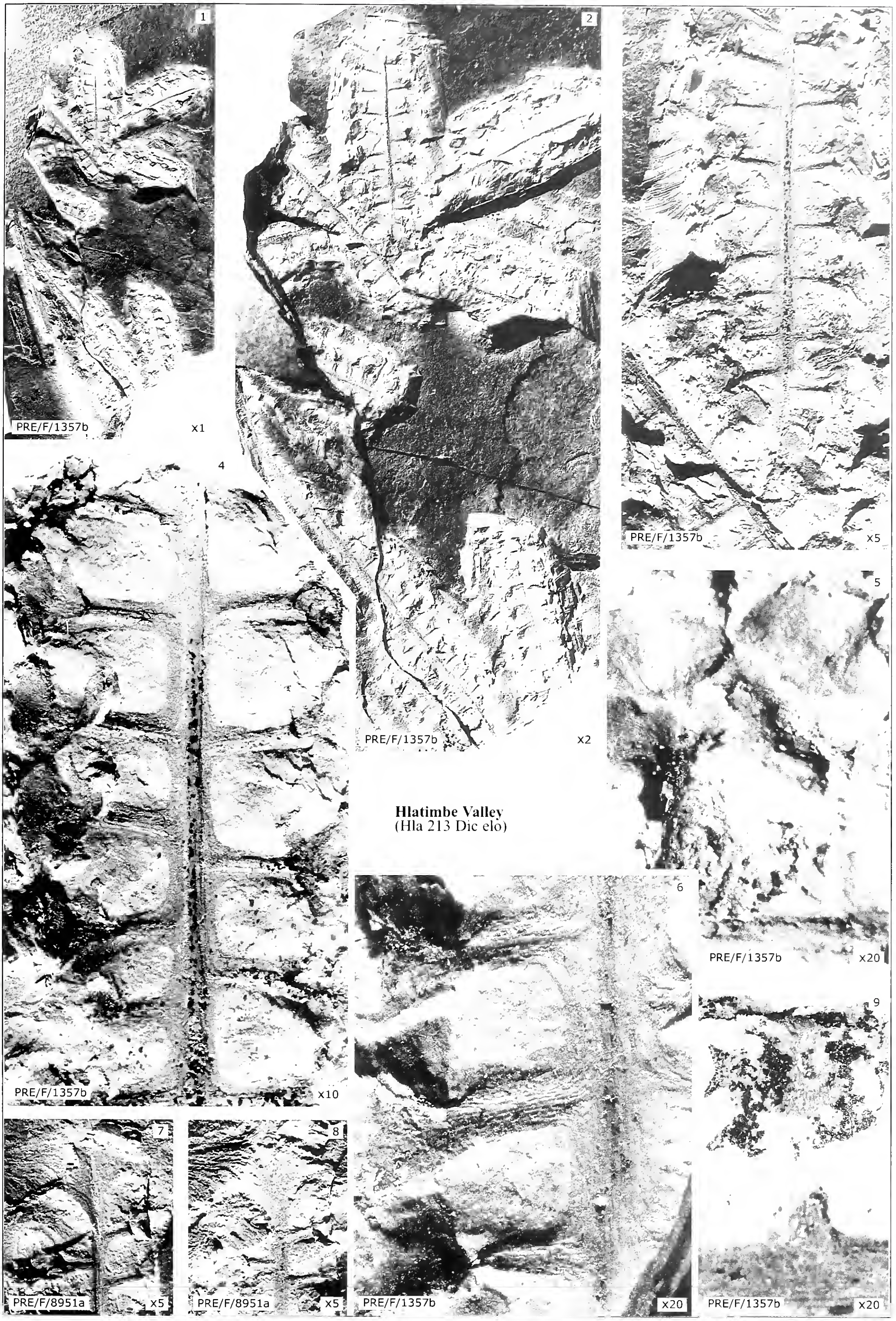


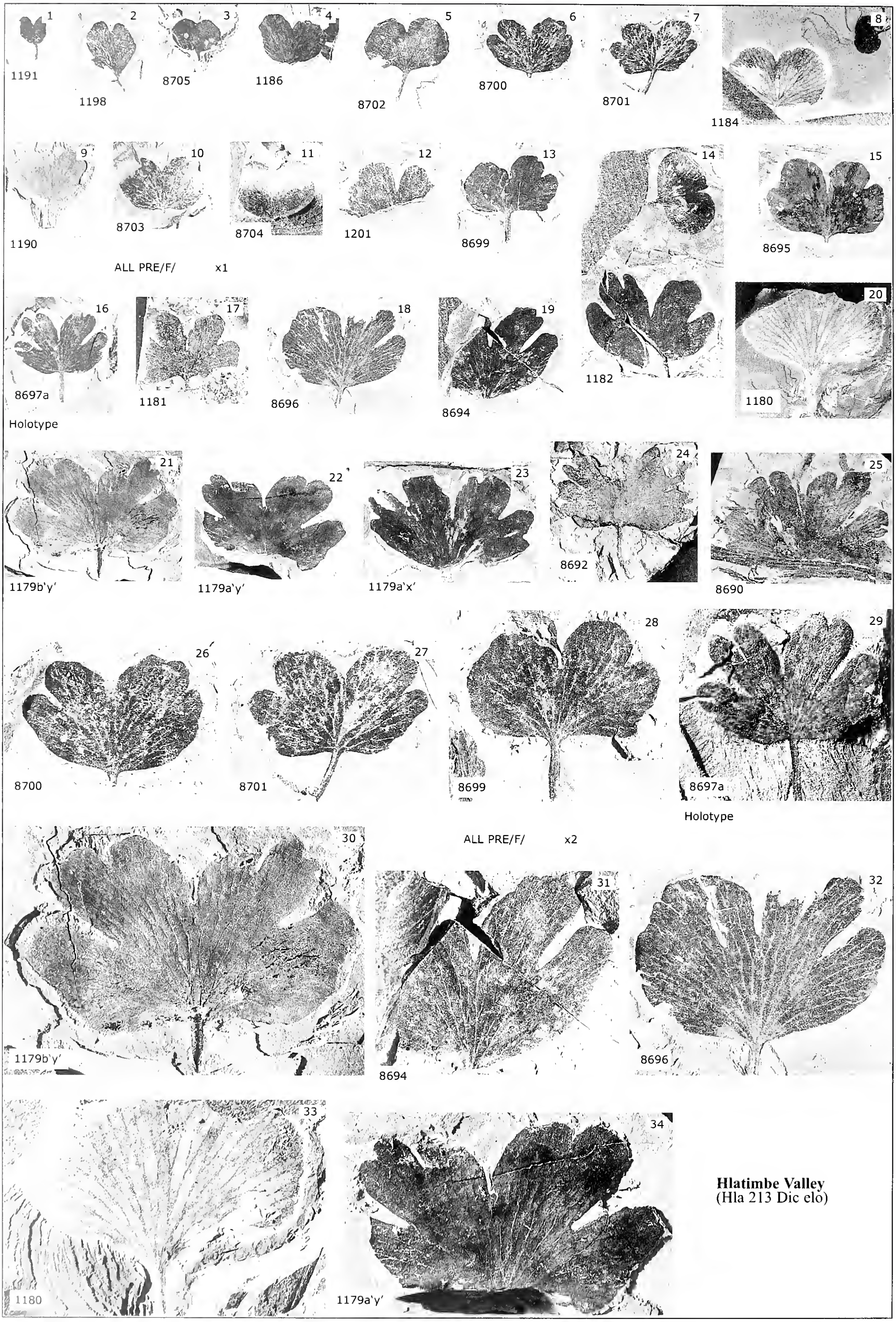


Holotype

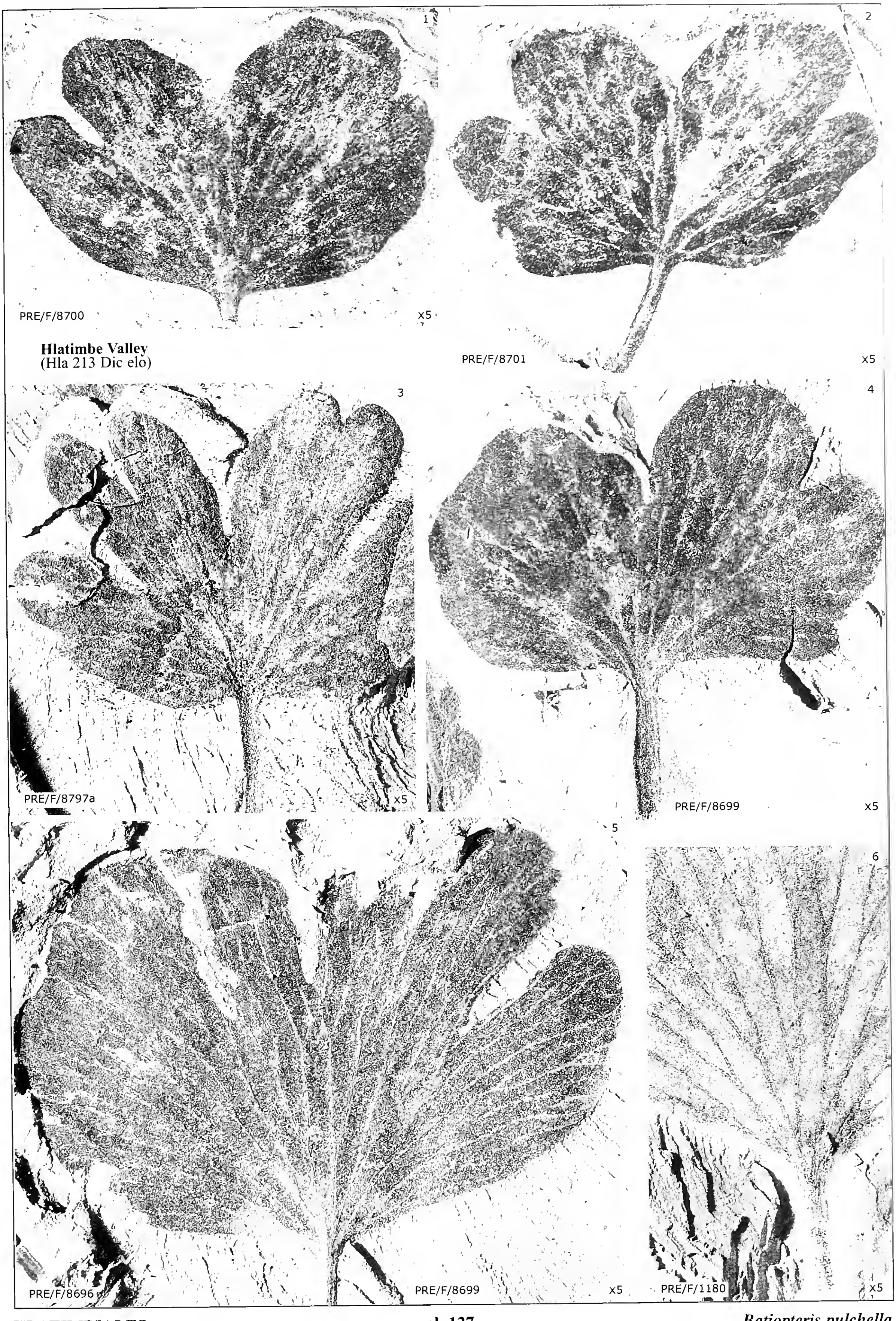
Hlatimbe Valley
(Hla 213 Dic elo)

Hlatimbia tommacleanii **pl. 124** **HLATIMBIALES**


1
PRE/F/1357b
x1
2
PRE/F/1357b
x2
3
PRE/F/1357b
x5
4
PRE/F/1357b
x10
5
PRE/F/1357b
x20
6
PRE/F/1357b
x20
7
PRE/F/8951a
x5
8
PRE/F/8951a
x5
9
PRE/F/1357b
x20
Hlatimbe Valley
(Hla 213 Dic elo)



Batiopteris pulchella **pl. 126** **HLATIMBIALES**



HLATIMBIALES **pl. 127** ***Batiopteris pulchella***

INCERTAE SEDIS class
INCERTAE SEDIS order
INCERTAE SEDIS family

Hystricia J.M.And. & H.M.And., gen. nov.

Type species
Hystricia perplexa J.M.And. & H.M.And., sp. nov.
Aasvoëlberg, Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis
A gymnospermous ovulate structure of (?)dorsiventral circular form, with a central 'gynoecium' of small ovuliferous cells surrounded by a perianth of bracts.

Generic characters
Strobilus: compact, circular, bilaterally symmetrical, dorsiventral, medium (*ca* 30 mm diam.); axis erect (*ca* 1.5 mm diam.); fertile head consisting of a central 'gynoecium' fringed by a perianth of bracts.
'*Gynoecium*': a honeycomb pack of numerous ovuliferous cells; bracts numerous, irregular, leafy, free and overlapping to base, each extending from a gynoecial cell.
Ovuliferous cell: minute (*ca* 0.5 mm diam.), pentagonal to hexagonal in surface section, with a central depression or micropyle.
Ovule: unknown.

Etymology
Hystricia—hystrix (Gr.), porcupine, with reference to the spine-like bracts surrounding the fruiting structure.

Global range: 1 sp., Gondwana, Tr. (CRN).
First & last: Molteno Fm.

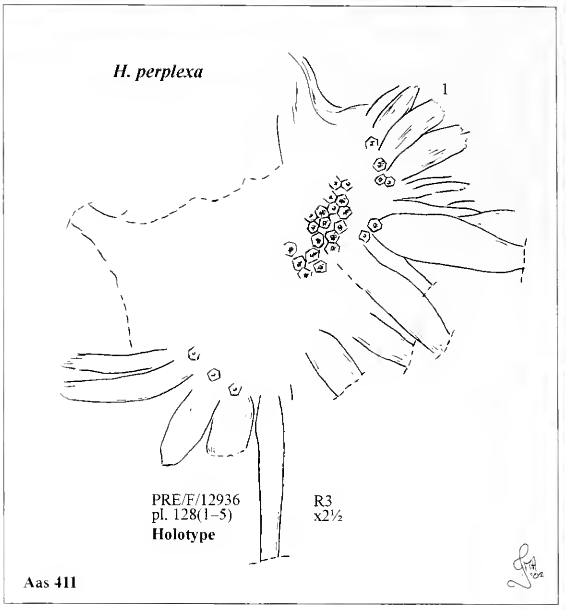
Gondwana Triassic occurrence
SAf—Karoo Basin, 1 TC (1 indiv.).

Molteno occurrence
Frequency (F): 1 TC (of 100 sampled in Molteno).
Diversity (D): 1 species.
Abundance (A): 1 indiv.
Aas 411 Dic/Sph: 1 indiv. in 512 man-hrs (1 per 51 man-days) vanishingly rare

Though we have devoted 512 man-hours to cleaving slabs from this highly significant lake-deposit site, no further sign of this uncertain taxon has been found.

Affiliated organs—unknown.

Classification & comparison
Suprageneric classification (incertae sedis/incertae sedis)
Hystricia, being represented by a solitary, fragmentary, unclear impression fossil, can be classified only with considerable doubt. It bears a superficial resemblance to the genus *Ottokaria* of the Permian Ottokariopsida. It differs in having a fringe of large, entirely free bracts and a head of numerous far smaller ovuliferous 'cells'. There is also a resemblance to the Triassic Bennettitalean genera '*Williamsonia*', *Sturianthus* and *Bennetticarpus*, but these are all radially symmetrical and show a peltate attachment of the pedicel. Although the features of *Hystricia* suggest that it could be placed in the Ottokariopsida or the Bennettitopsida, we place it in the class incertae sedis until more details are forthcoming.



Hystricia perplexa J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/12936; pl. 128(1–5).
Assemblage (TC): Aas 411 Dic/Sph; Aasvoëlberg.
Preservation: partial 'gynoecium', no counterpart; impression in thinly laminated, strongly baked, yellowish grey shale with very good cleavage.

Reference palaeodeme—as for holotype.

Sister palaeodemes—nil.

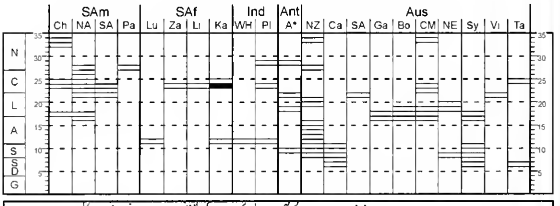
Species diagnosis—as for genus.

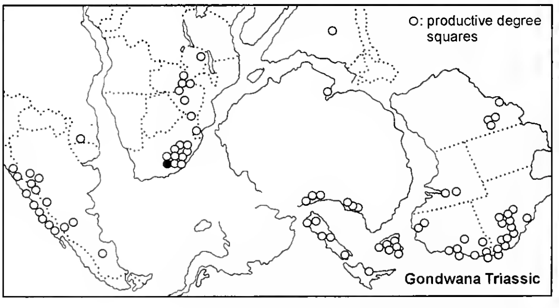
Species description—as for genus.

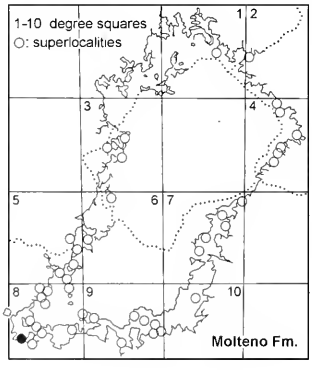
Etymology
perplexa (Lat.)—confused, intricate, with reference to the enigmatic structure of the only available specimen.

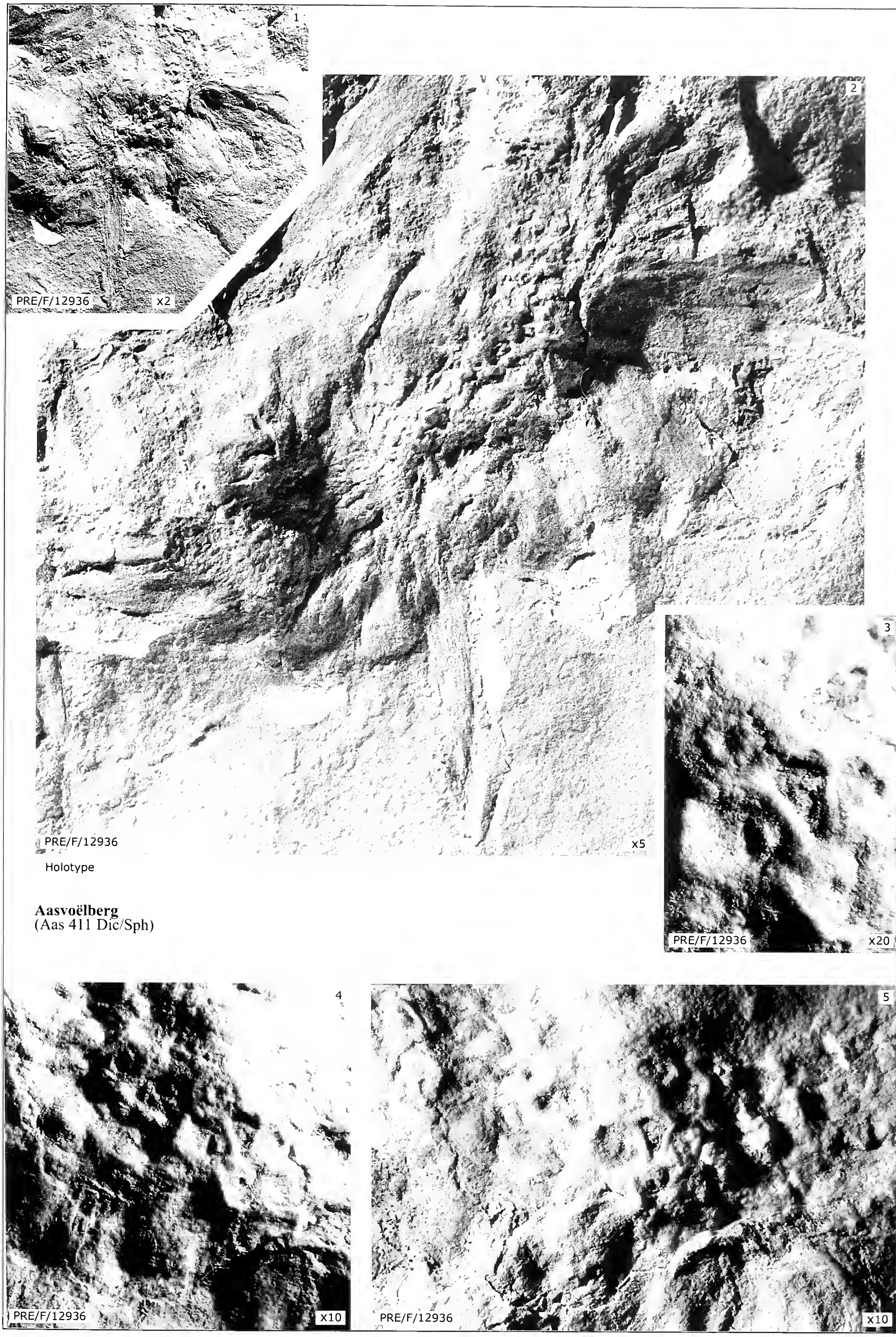
Comment & comparison—see for genus.

GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION









Aasvoëlberg
(Aas 411 Dic/Sph)

INCERTAE/INCERTAE pl. 128 *Hystricia perplexa*

INCERTAE SEDIS class
INCERTAE SEDIS order
INCERTAE SEDIS family

Saportaea Fontaine & I.C.White 1880

Type species
Saportaea salisburioides Fontaine & I.C.White 1880
West Virginia, USA; Pennsylvanian, Carboniferous.

Generic concept
A gymnospermous leaf of uncertain class with a long gracile petiole and lamina divided into 2 arcuate entire or deeply incised lobes with prominent inner-marginal vein and subparallel forking secondary veins.

Generic characters (based only on the 2 Gondwana Triassic species)
Leaf: small to large, bipartite, with 2 primary arcuate lobes subtended by a long slender petiole; lamina entire or deeply divided into dichotomising narrowly oblong to linear segments; venation consisting of a prominent vein following the inner arcuate lobe margin and closely spaced lateral veins, arching, subparallel, forking but not anastomosing.
Cuticle: see And. & And. (1989, p. 530); this vol., tf. 5 opposite.

Eponymy
Saportaea—after G. Saporta, a 19th century French palaeobotanist.

Global range: several spp., Pangaea, L.P–U.Tr.

Gondwana Triassic occurrence
Frequency (F): 3 degree squares (of the 84 across Gondwana).
Ubiquity (U): 3 continents (of 5 comprising Gondwana).
Diversity (D): 2 foliage species.
Abundance (A): <1% (the norm in Molteno TCs).
Longevity (L): 9 myrs (Lower Anisian to Lower Carnian).
Colonisation success: FUDAL rating 3/3/2/–/9 = 17.
Limited success (Grade 2); *Saportaea* was the 19th most prominent genus in the Gondwana Triassic; it was relatively ubiquitous, diverse and long-lived, but infrequent and rare.
Endemism: the 2 species are single-assemblage endemics.

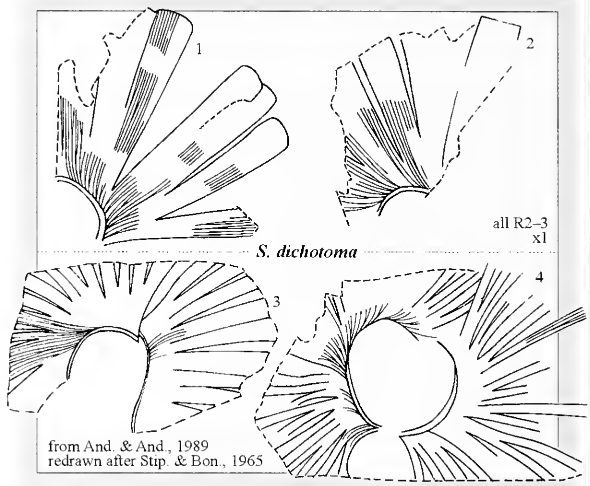
Molteno occurrence
Frequency (F): 1 TC (of 100 sampled in the Molteno).
Diversity (D): 1 species.
Abundance (A): 1 indiv.; vanishingly rare.
Habit: most likely herbaceous undergrowth.
Preferred habitat: *Dicroidium* riparian forest.

Affiliated organs
Unknown.

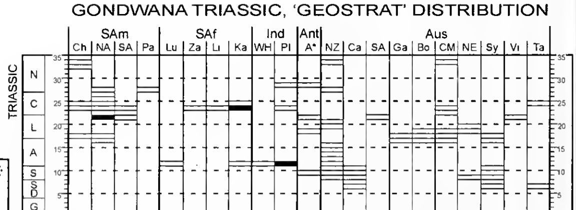
Classification & comparison
Intergeneric comparisons
Gondwana Triassic gymnosperm genera—Saportaea, whose reproductive organs remain unknown, could conceivably be an early member of the Dipteridaceae. It was placed by Stipanicic & Bonetti (1965) in the Ginkgoales in view of the obvious parallels in the dichotomising nature of the lamina and venation. However, the prominent vein that follows the inner margin of the arcuate lobes clearly distinguishes it from *Ginkgo*-like leaves. We prefer to place it under incertae sedis (order level). The very fragmentary cuticular remains available show gently curved cell walls, but no further details to suggest relationships.
Saportaea, with its bipartite leaf with two primary arcuate lobes subtended by a long slender petiole, is unlike any other gymnospermous leaf.

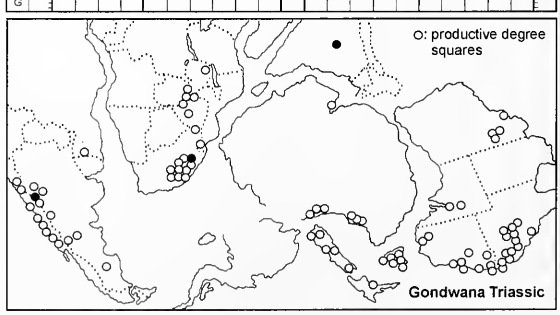
Other genera—The basic architecture of *Saportaea* is found also in the fern family Dipteridaceae (U. Triassic to present). The fronds of the latter differ in that they bear sori, have lamina segments that are often pinnate, and generally show reticulate venation. The member of the family that superficially looks most like *Saportaea* is the extant *Dipteris conjugata*, but with its bifurcating lamina and reticulate venation (Andrews *et al.* 1970, f. 265) it is quite distinct.

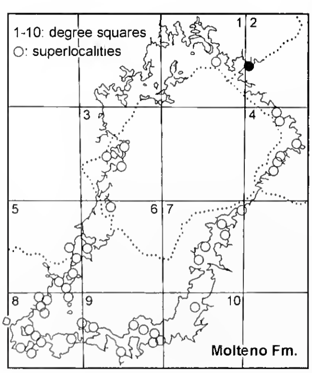
Interspecific comparisons
Saportaea is a rare, nondiverse genus recognised from the L. Permian to U. Triassic of the USA, China, Australia and S. Africa. Superficially, the various species appear generically related, but this cannot be confirmed owing to lack of cuticular information or fruiting bodies. *S. magnifolia*, the single species described from the Molteno, is separated mainly on gross morphological characters (And. & And. 1989, p. 530).

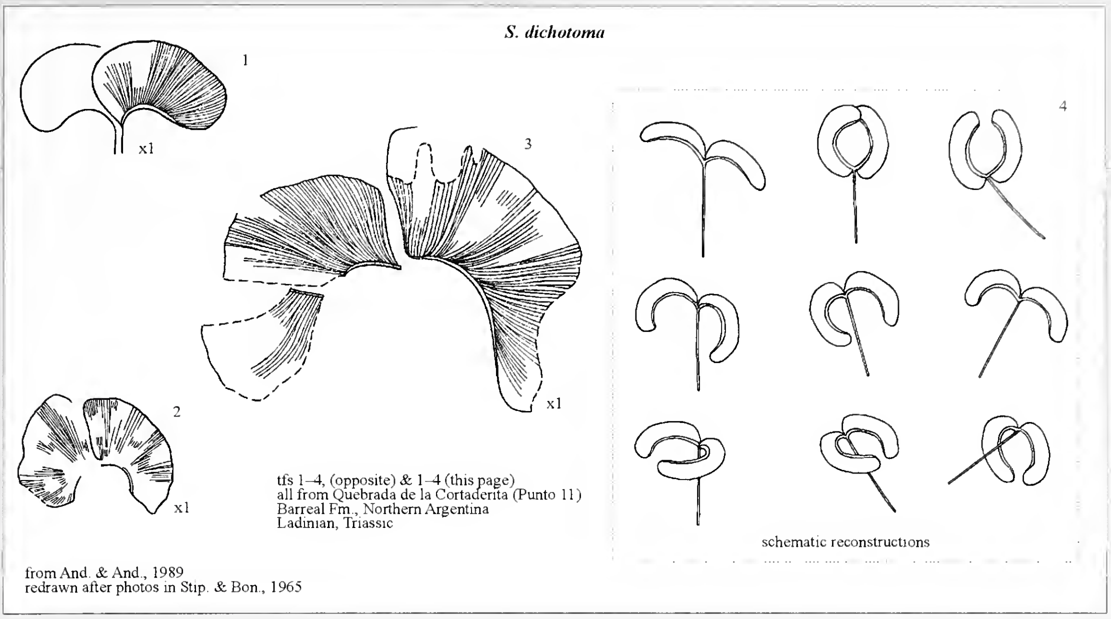


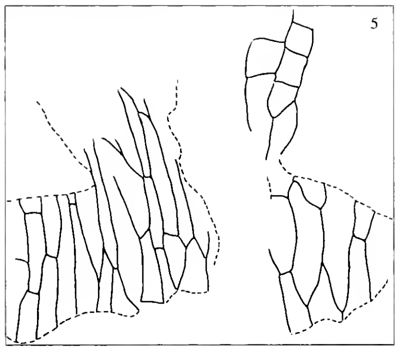
GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION







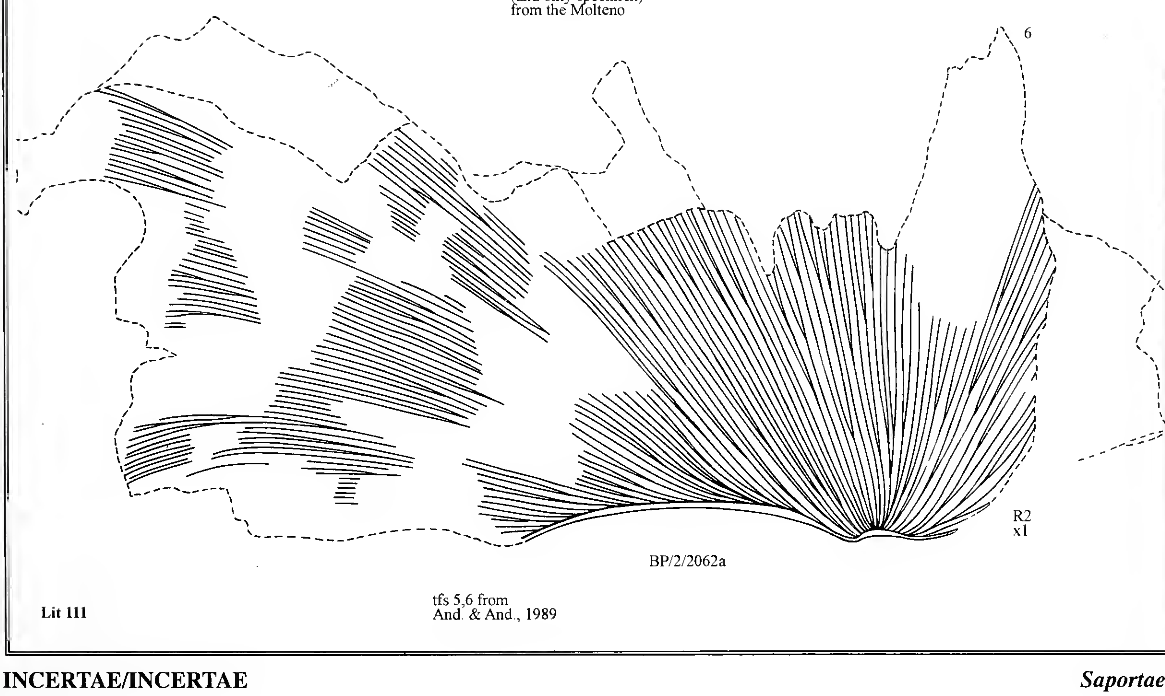




BP/2/2062 x100

S. magnifolia

the single species
(and only specimen)
from the Molteno



BP/2/2062a

Lit 111

tfs 5,6 from
And. & And., 1989

INCERTAE SEDIS class
INCERTAE SEDIS order
INCERTAE SEDIS family

Linguifolium E.Arber 1913

Type species
Linguifolium lillieanum E.Arber 1913.
Mt. Potts, New Zealand; Ladinian, Triassic

Generic concept
A gymnospermous leaf of uncertain class with linear-elliptic lamina, entire margins and a midrib with steep forking secondary venation.

Generic characters
Leaf: small to medium, linear-elliptic to narrowly elliptic or oblanceolate; apex sharply acute to obtuse; lamina entire, tapering very gradually to base; midrib strong, tapering out short of apex; veins moderately to well spaced, at steep angle to midrib and curving slightly, forking once or twice but not anastomosing.
Cuticle: see And. & And. (1989, p. 520); this vol., tfs 1, 2 opposite.

Etymology
Linguifolium—lingua (Lat.), tongue; *folium* (Lat.), leaf.

Global range: 5 spp., Gondwana, L.–U. Tr. (SCY–NOR).
First: *Linguifolium* sp. *(Taeniopteris)* (Walkom 1925a); Turrimetta Head, L. Newport Fm., Sydney, Australia.
Last: *Linguifolium arctum* (Retallack 1985); Highfield Homestead, ?Fm., Nelson Syncline, New Zealand.

Gondwana Triassic occurrence
Frequency (F): 18 degree squares (of the 84 across Gondwana).
Ubiquity (U): 4 continents (of 5 comprising Gondwana).
Diversity (D): 5 foliage species.
Abundance (A): <1% (the norm in Molteno TCs).
Longevity (L): 25 myrs (upper Scythian to Upper Norian).
Colonisation success: FUDAL rating 18/4/5/–/25 = 54.
Intermediate success (Grade 3); *Linguifolium* was the 6th most prominent genus in the Gondwana Triassic; it was of moderate frequency, ubiquity and abundance, had marked longevity in the Triassic, but lacked diversity.
Endemism: The five species may well come to be regarded as one widespread polymorphic species in the future.

Molteno occurrence
Frequency (F): 8 TCs (of 100 sampled in the Molteno).
Diversity (D): 1 species.
Abundance (A): occasional (1%) in 1 TC; rare to extremely rare (<1%) in other 7 TCs.
Habit: possibly a herbaceous pioneer.
Preferred habitat: *Dicroidium* riparian forest (5 of 8 TCs).

Affiliated organs (New Zealand)
Female strobilus: seeds only, *Carpolithus mackayi*, Grade 3 (Mut. occ.) (see And. & And. 1989, p. 520).
Male strobilus: unknown.

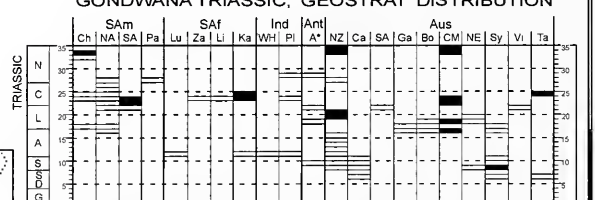
Classification & comparison
Intergeneric comparisons
Gondwana Triassic genera—As a simple more or less linear to narrowly elliptic leaf with clear midrib, *Linguifolium* is similar to *Yabeiella* and *Gontriglossa*, but the former has simple bifurcating side veins while the latter has anastomosing veins. The cuticle of *Linguifolium*, with straight to gently curving cell walls, differs from *Yabeiella* and *Gontriglossa* which both have meandering cell walls.

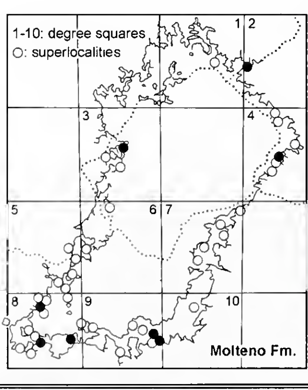
Other genera—Retallack (1980a) compared *Linguifolium* with a wide range of somewhat similar genera of all ages and geographic origin. Among those considered were *Blechnoxylon* Etheridge (wood with leaves attached, 'Permo-Carboniferous', NSW, Australia), *Phyllopteroides* Medwell (L. Jurassic, Victoria, Australia), *Tatarina* Meyen (U. Permian, Kirovskaya Oblast, USSR), *Lesleya* Lesquereux (Pennsylvania, USA), and *Palaeovittaria* Feistmantel (Permian, Raniganj, India). Retallack recognised sufficient differences to treat *Linguifolium* as an independent genus.

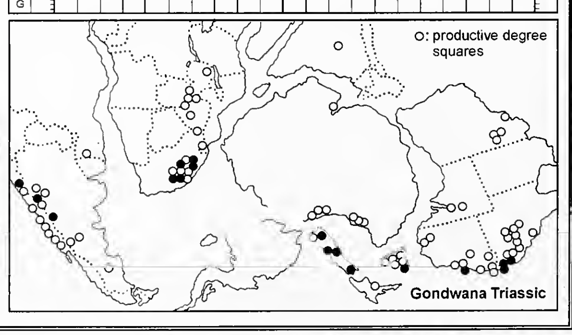
Interspecific comparisons
The five species of *Linguifolium* recognised from the Gondwana Triassic (And. & And. 1989) fall readily within the compass of a natural genus on the basis of their leaf macromorphology. The available palaeodemes of the five species present a complex series of overlapping morphological ranges and undoubtedly represent a single genus if not a single polymorphic species.

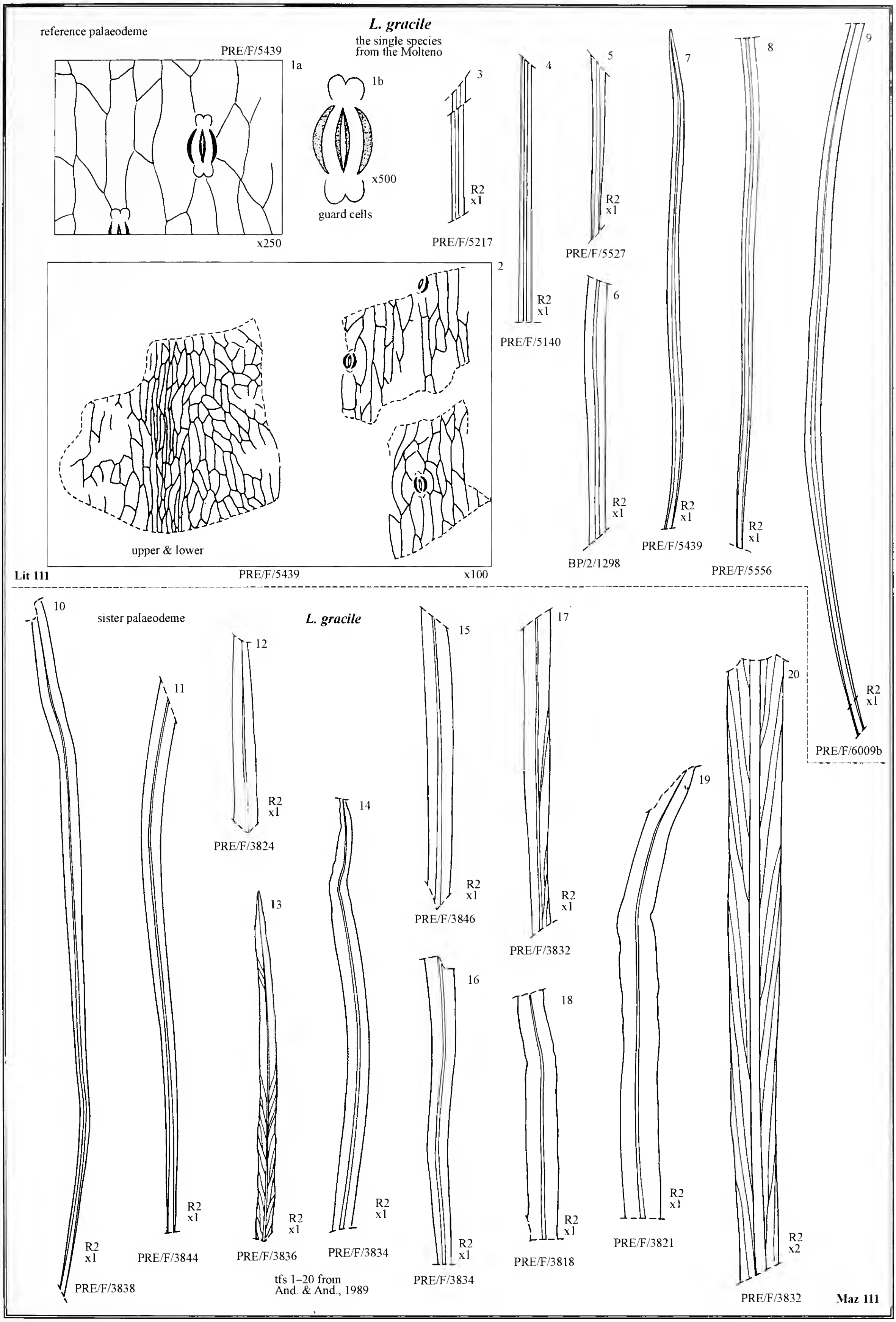
Cuticle is known only for the Molteno species *L. gracile*, while the affiliated seed (*Carpolithus mackayi*), apparently well established (Retallack 1980a), remains known only for the New Zealand species.

GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION








reference palaeodeme
L. gracile
the single species
from the Molteno
PRE/F/5439
1a
x250
1b
x500
guard cells
3
R2
x1
PRE/F/5217
4
R2
x1
PRE/F/5140
5
R2
x1
PRE/F/5527
6
R2
x1
BP/2/1298
7
R2
x1
PRE/F/5439
8
R2
x1
PRE/F/5556
9
R2
x1
PRE/F/6009b
2
upper & lower
PRE/F/5439
x100
Lit 111
10
sister palaeodeme
R2
x1
PRE/F/3838
11
R2
x1
PRE/F/3844
L. gracile
12
R2
x1
PRE/F/3824
13
R2
x1
PRE/F/3836
14
R2
x1
PRE/F/3834
15
R2
x1
PRE/F/3846
16
R2
x1
PRE/F/3834
17
R2
x1
PRE/F/3832
18
R2
x1
PRE/F/3818
19
R2
x1
PRE/F/3821
20
R2
x2
PRE/F/3832
tfs 1–20 from
And. & And., 1989
Maz 111

BENNETTITOPSIDA
FREDLINDIALES J.M.And. & H.M.And., ord. nov.
FREDLINDIACEAE J.M.And. & H.M.And., fam. nov.

Fredlindia J.M.And. & H.M.And., gen. nov.

Type species
Fredlindia fontifructus J.M.And. & H.M.And., sp. nov.
Aasvoëlberg, Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis
A bennettitopsid ovulate strobilus of compact cone-like form; with bilaterally symmetrical 'gynoecia' borne in a series of whorls.

Generic characters
Strobilus: simple, compact, cone-like, medium (120 x 35 mm); axis stout (7 mm diam. at base), markedly tapering; 'gynoecia' in *ca* 6 whorls of 3–8 units along axis.
'Gynoecium': bilaterally symmetrical, tongue-shaped lamina, apparently succulent, medium (25 x 10 mm); peduncle short, stout; ovuliferous 'cells' (megasporophylls) abaxial, a honeycomb aggregate of numerous segments.
Ovuliferous 'cell': columnar, tapering gradually proximally, pentagonal to hexagonal in section, (?)uni-ovulate; micropyle distinct, circular, central with radial striae at distal face.

Etymology
Fredlindia—in honour of Fred and Linda Terblanche, on whose farm Aas 411 occurs.

Global range: 1 sp., Gondwana, Tr. (CRN).
First: *Fredlindia* sp. indet. (*Equisetites*? sp.) (Jones & De Jersey 1947); Tivoli stage, Ipswich CM, Australia.
Last: Molteno Fm.

Gondwana Triassic occurrence
SAf—Karoo Basin, 3 TCs (16 indivs).
Aust—Clarence-Moreton Basin, 2 TCs (5 indivs).

Molteno occurrence
Frequency (F): 3 TCs (of 100 sampled in the Molteno).
Diversity (D): 1 species.
Abundance (A): 16 indivs total; very rare to extremely rare.

Kon 222 Dic odo:	3 indivs in	40 man-hrs	(1 per	1 man-day)	very rare	
Aas 411 Dic/Sph:	11 "	" 512 "	(1 "	5 ")	extremely rare	
Bir 111 Sph 2 spp:	2 "	" 550 "	(1 "	27 ")	"	"

The potential for finding further *Fredlindia* specimens (other than at new localities) rests largely at Aas 411. Although the yield there, to date, has been very low—one specimen per five man-days cleaving—the site is extensive, easy to excavate and the well-bedded sheets of hard shale are readily cleaved. The yield at Bir 111, a very similar deposit, is five times lower, while Kon 222, with a yield five times higher than Aas 411, is a site of very limited extent and is apparently mined out.

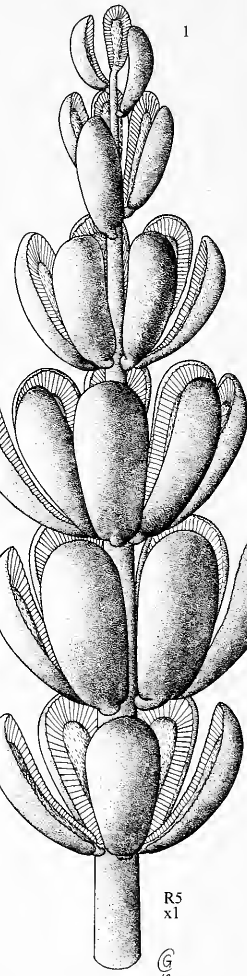
Affiliated organs
Male strobilus: *Cycadolepis/Weltrichia*—Grade 3 (Mut. occ.).
Foliage: *Halleyoctenis*—Grade 3 (Kin. reinf., Mut. occ.).

Classification & comparison
Suprageneric classification (Fredlindiaceae/Fredlindiales)
The *Fredlindia* 'gynoecia' are very like those of the Bennettitales in being characterised by a honeycomb of ovuliferous 'cells' and/or interseminal scales, but differ markedly in being bilaterally symmetrical and in being borne in a series of whorls. Including the genus in the Bennettitales would necessitate major alterations to that well-defined and understood order. We prefer to erect a new order for the genus *Fredlindia* and to include it with the Bennettitales in the class Bennettitopsida.

If the affiliation of the foliage *Halleyoctenis* with *Fredlindia* proves true, then this phylogenetic position is further substantiated. The early bennettitalean leaf genera *Laurozamites* and *Pterophyllum* of the Laurasian Late Triassic are clear intermediates between *Halleyoctenis* and the typical bennettitalean leaves of the Jurassic (see further detail under *Halleyoctenis*).

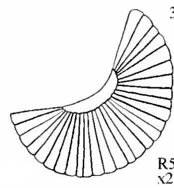
Intergeneric comparison (Gondwana Triassic)
Fredlindia is unique.

F. fontifructus


1

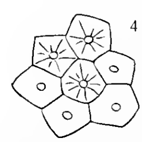
based on
Aas 411 (for apex)
PRE/F/12749
Kon 222 (for base)
PRE/F/2270

R5
x1


3

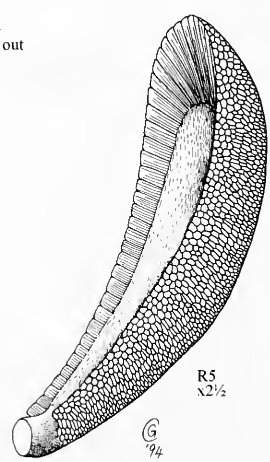
R5
x2½

Cross section of "gynoecium"
with sterile receptacle and radiating megasporophylls


4

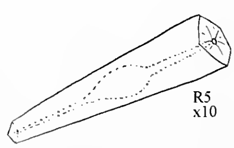
R5
x10

External view of "gynoecium"
showing pentagonal-hexagonal megasporophylls and schematic representation of cells radiating out from central micropyle


2

R5
x2½

"gynoecium"


5

R5
x10

Ovuliferous "cell" (megasporophyll)
with hypothetical position (not seen) of micropylar tube and ovule

Reconstructions

Strobilus

The reconstruction (tf. 1 opposite) is based primarily on PRE/F/12749 (the holotype from Aas 411, pl. 129) and PRE/F/2270 (from Kon 222, pl. 134)—the former consisting of the distal five whorls through to the clearly preserved apex of the strobilus, and the latter of the proximal whorl, including the complete stalk. The drawing is a combination of these two specimens and results in a strobilus with four perfect whorls and two irregular whorls to the tip. The number of whorls that would comprise an average strobilus is not known and could well be greater than that shown in our reconstruction.

'Gynoecium'

The original thickness of the individual 'gynoecium' is uncertain. Though all strobili are preserved three-dimensionally, the 'gynoecia' are mostly preserved without significant dorsiventral thickness. The Kon 222 specimens (pl. 134) suggest that they were fleshy in life and were flattened during fossilisation. The cross section of the 'gynoecium' (tf. 3 opposite) is based on these Kon 222 specimens.

Ovuliferous 'cell'

The 'cells' are most readily interpreted as elongate circumseminal scales/sheaths, apparently fleshy, embedding a long tubular micropyle and an ovule of unknown shape and size—reminiscent of the bennettitaleans. They have been reconstructed to show the possible position of the micropylar tube and ovule (tf. 5 opposite). Whether these 'cells' all had ovules or whether some proportion of them were sterile is not known.

Gondwana Triassic occurrence (elaborated)

Australia

The individuals recorded for Australia in the hypodigm (Tab. 61) are all described in the original literature (Shirley 1898; Jones & De Jersey 1947; Hill *et al.* 1965) as being of sphenophyte origin, either as cones, cone-scars or nodal diaphragms. Although the published illustrations are poor, we consider it very likely that the three Australian specimens all represent detached megasporophylls of *Fredlindia* strobili.

The material derives from two localities in the Clarence-Moreton Basin, Queensland: Denmark Hill (Locality 39 or 39A of Jones & De Jersey 1947), and portion 179 of parish Chuwar (Locality 6), from the Blackstone and Tivoli Stages respectively. It is unclear from the descriptions whether any of the specimens are compressions that might offer potential for cuticular study.

Beyond Gondwana Triassic

The only bennettitopsid genus with 'gynoecia' attached to an axis is *Westerheimia* from the Upper Triassic of Lunz, Austria. Crane (1986) described *W. pramelreuthensis* as bearing 'several bennettitalean "gynoecia", each composed of interseminal scales and ovules'. This differs from *Fredlindia* in lacking a whorled structure and in its much smaller size.

Evidence for affiliation of organs

Mutual occurrence

Halleyoctenis is the most probable foliage affiliate of *Fredlindia*. It is an abundant to extremely rare component of 10 Molteno TCs (Tab. 60). *Fredlindia* is a very rare to extremely rare element, known from only three Molteno TCs—each of which yields *Halleyoctenis*.

Kindred reinforcement

Supporting the evidence for 'mutual occurrence' is that both *Halleyoctenis* and *Fredlindia* show certain features hinting clearly at a phylogenetic link with the order Bennettitales (see notes under 'Classification' opposite and on p. 344).

Australia

Halleyoctenis, as currently known, displays a markedly disjunct distribution, appearing only in S. Africa and in Queensland. *Fredlindia* has the same disjunct distribution, being unknown from any of the other Gondwana continents.

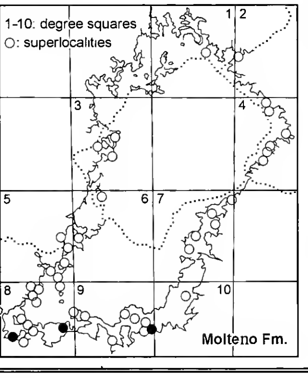
The leaf genus *Halleyoctenis* is widespread in the Middle to Upper Triassic formations of the Clarence-Moreton Basin, Queensland (And. & And. 1989, p. 327, Tab. 4.38). It occurs in both the Denmark Hill and Chuwar (Loc. 6) assemblages which yield the presumed *Fredlindia* specimens (Jones & De Jersey 1947, pp. 45–48, 66, 70; And. & And. 1989, p. 365).

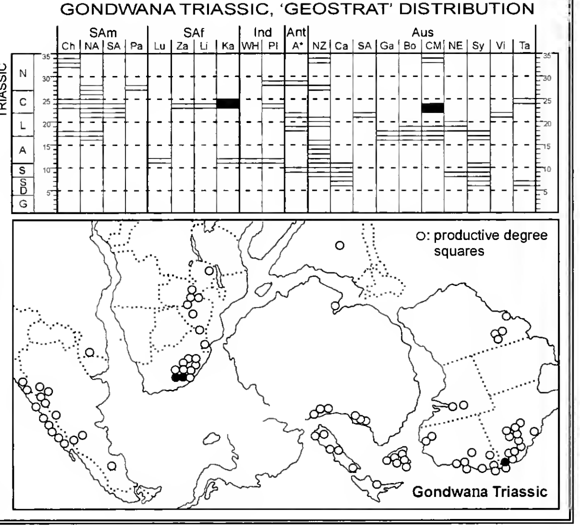
Intactness & preservation of cones (Molteno)

All but two of the 13 specimens are detached isolated megasporophylls; PRE/F/2270 from Kon 222 consists of a proximal end of a strobilus (stalk and lower whorl of megasporophylls); the holotype PRE/F/12749a,b from Aas 411 consists of the greater part of a strobilus, but with the proximal end missing. The preservation in all three TCs is as 3D impression/moulds.

Adaptive radiation (Molteno diversity)

The collections of *Fredlindia*, mostly detached 'gynoecia' from the Molteno and two Queensland assemblages, are insufficient to justify the recognition of more than one species. Considering the fact that three species are currently recognised for the supposed foliage affiliate, *Halleyoctenis*, it is likely that a more comprehensive sample of *Fredlindia* material would reveal more diversity within the genus.





Fredlindia fontifructus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/12749a,b; pls 129(1–5), 130(1, 2).
Assemblage: Aas 411, Dic/sph, Aasvoëlberg.
Preservation: fairly complete strobilus, part and counterpart, including 5 whorls of 'gynoecia'; proximal portion of strobilus not available (broken off at a joint in the rock); impression in thinly laminated, strongly baked, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage: as for holotype.
Specimens: 11 individuals; including the holotype and 10 isolated, detached 'gynoecia', pls 129–132.

Sister palaeodemes—2 (both listed)
Kon 222 Dic odo: 3 indivs (1 intact, 1 partial, 1 isolated), pl. 134.
Bir 111 Sph 2 spp: 2 indivs (2 isolated), pl. 133.

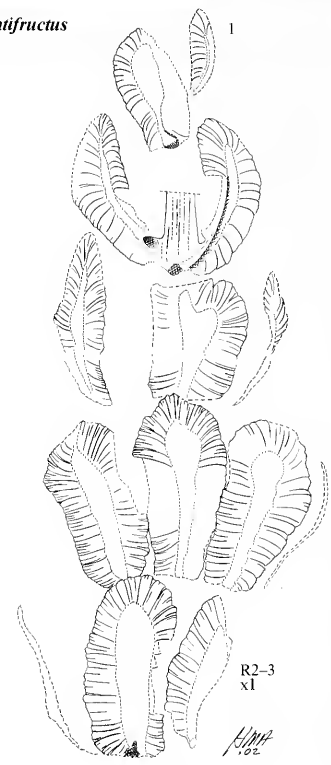
Specific diagnosis—as for genus.

Specific characters—as for genus.

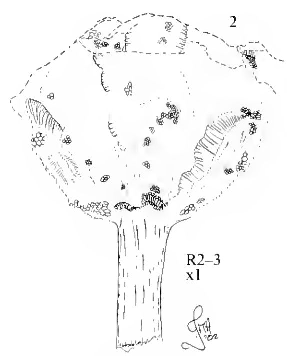
Etymology
fontifructus—*fontis* (Lat.), source, spring, fountain; *fructus* (Lat.), fruit, with reference to this fruit being near the fountainhead of the Bennettitopsida.

Comment & comparison
It is possible that the three available palaeodemes represent more than a single species, but the material at hand is too sparse and incomplete to make a judgement.

F. fontifructus



Aas 411 — PRE/F/12749a,b pl. 129(1,2) **Holotype**



Kon 222 — PRE/F/2270a pl. 134(1,2)

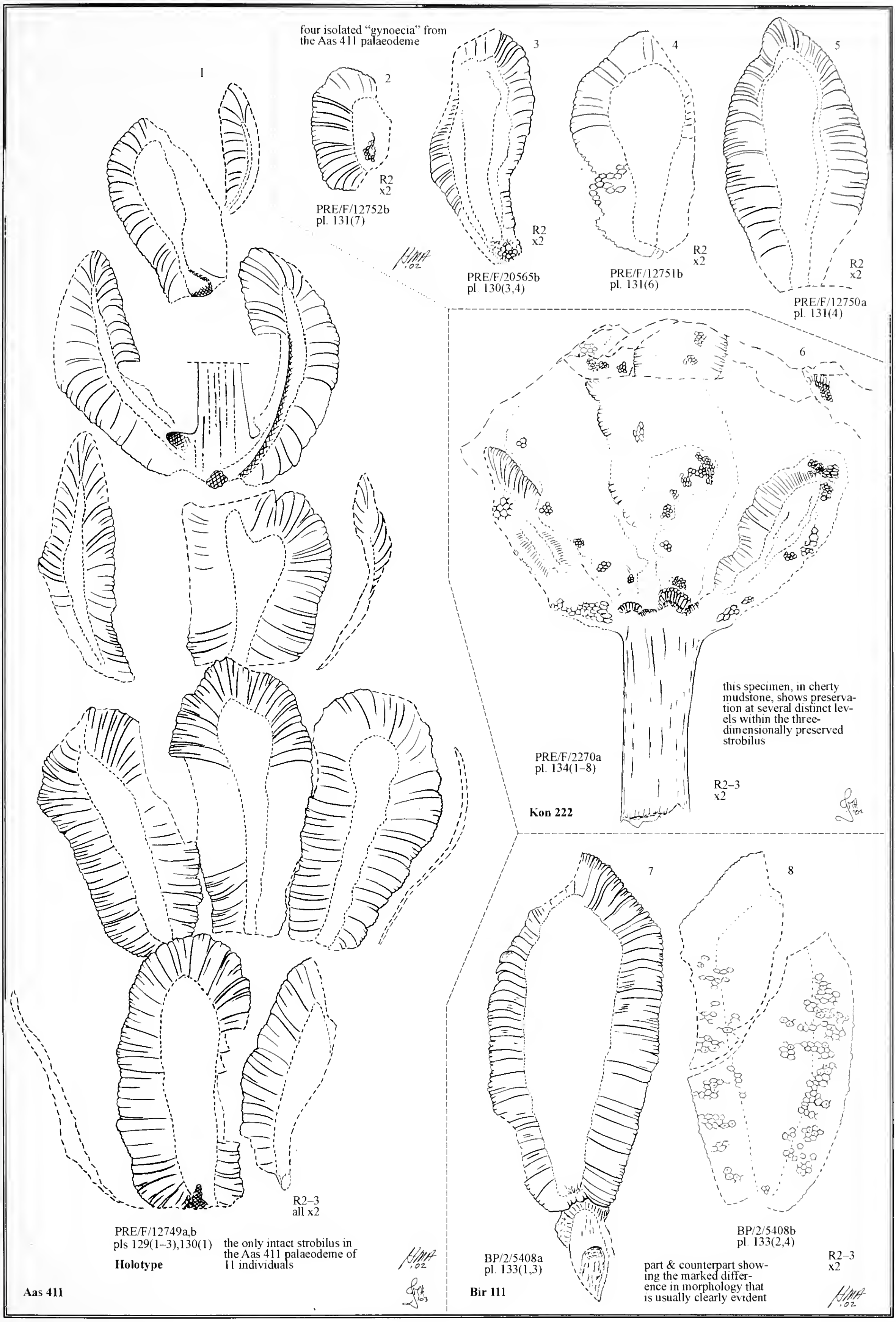
assemblages (taphocoenosis)		*Halleyoctenis*	*H. brachypinnata*	" *megapinnata*	*Fredlindia* ♀	*Cycadolepis* ♂	*Weltrichia* ♂	*Leguminanthus* ♂
Bir 311	Hei/Sph	1	-	1	-	-	-	-
" 111	Sph 2spp	6	3	3	2	1	-	-
Kon 223	Dic odo	**15**	**8**	**7**	-	-	-	-
" 222	Dic odo	**8**	**8**	-	3	10	1	5
" 111	Dic odo	10	10	-	-	-	-	-
Pen 321	Dic/Ris	**5**	**5**	-	-	-	-	-
" 211	Dic/Equ	**2**	**2**	-	-	-	-	-
" 431	Dic/Equ	2	2	-	-	-	-	-
Lit 111	Dic/Hei	8	-	8	-	-	2	-
Aas 411	Dic/Sph	40	8	32	11	3	-	-
Total TCs		10	8	5	3	3	2	1
Total indivs		%	%	%	16	14	3	5

Tab. 60. ***Fredlindia/Halleyoctenis*, Molteno occurrence**

Tab. 61

***FREDLINDIA* HYPODIGM, Gondwana Triassic occurrence**

AUTHOR	SUBREGION	FORMATION	LOCALITY	NAME	Indivs ILLUSTRATION	Species: Mo. *F. fontifructus*	*F. spp. indet*	Intactness: Intact strobili	Partial "	Isolated megasp.
AUSTRALASIA (Queensland, Clarence-Moreton Basin)										
1898 Shirley	Ipswich/Esk CM5	24 Blackstone St.	Denmark Hill	*Equisetites mortonensis*	1 f 18(3)	-	1	-	-	1
1947 Jones & de J.	" "	23 Tivoli St.	Chuwar (Loc.6)	*Equisetites* ?sp.	1 tf 1, pl 1(1)	-	1	-	-	1
1965 Hill *et al.*	" "	24 Blackstone St.	Denmark Hill	*Neocalamites* cf. *carrerei*	1 pl T1(3)	-	1	-	-	1
SOUTH AFRICA (Karoo Basin)										
1978-1999 Anderson & Anderson Molteno literature not included in this table										



1
four isolated "gynoecia" from the Aas 411 palaeodeme
2
R2 x2
PRE/F/12752b pl. 131(7)
3
R2 x2
PRE/F/20565b pl. 130(3,4)
4
R2 x2
PRE/F/12751b pl. 131(6)
5
R2 x2
PRE/F/12750a pl. 131(4)
6
this specimen, in cherty mudstone, shows preservation at several distinct levels within the three-dimensionally preserved strobilus
PRE/F/2270a pl. 134(1–8)
R2–3 x2
Kon 222
7
8
R2–3 all x2
PRE/F/12749a,b pls 129(1–3),130(1)
Holotype
the only intact strobilus in the Aas 411 palaeodeme of 11 individuals
Aas 411
BP/2/5408a pl. 133(1,3)
Bir 111
BP/2/5408b pl. 133(2,4)
part & counterpart showing the marked difference in morphology that is usually clearly evident
R2–3 x2

Weltrichia Braun 1847 (emend. T.M.Harris 1969)

Type species
Weltrichia mirabilis Braun 1847.
Origin of type material apparently obscure.

Generic characters
'Flower' (*sensu* Harris 1969, and others for 'a *Williamsonia* fructification'): cup-shaped with numerous (8–?30) uniform tapering lobes.
Microsporophyll: an individual lobe; pollen sacs borne on inner surface.
Pollen sac: of 2 equal valves; microsporangia in a single row per valve, opening inwardly.
Pollen: oval, monocolpate.

Etymology
Weltrichia—source of name unknown.

Global range: several spp., Pangaea, U. Tr.–U. K.

Gondwana Triassic occurrence
SAf—Karoo Basin.

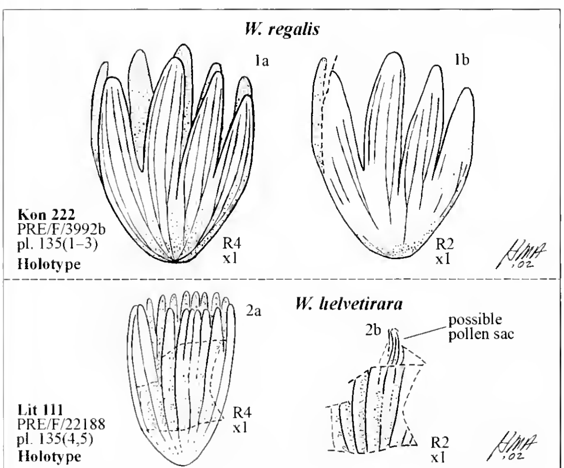
Molteno occurrence
Frequency (F): 2 TCs (of 100 sampled in Molteno).
Diversity (D): 2 species.
Abundance (A): 3 indivs total; very rare to extremely rare.

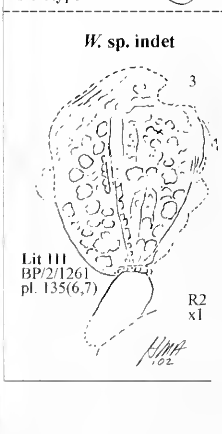
Kon 222:	1 indiv. in	40 man-hrs	(1 per 4 man-days)	very rare
Lit 111:	2 " "	550 "	(1 " 27 ")	extremely rare

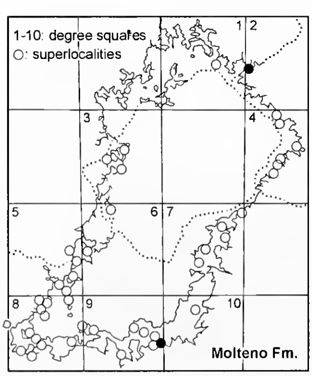
Affiliated organs
Female strobilus: *Fredlindia*—Grade 3 (Mut. occ.).
Foliage: *Halleyoctenis*—Grade 3 (Kin. reinf., Mut. occ.).

Classification & comparison
Suprageneric classification (Fredlindiaceae/Fredlindiales)

The Molteno material included here gives no direct indication of whether this is a male or female structure. The specimens are placed in *Weltrichia* (a male bennettitalean 'flower') on the basis of general similarity. *W. regalis* is, perhaps, close to *W. whitbiensis* from the Yorkshire Jurassic (Harris 1969, pl. 7, figs 4, 5).







Weltrichia regalis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/3992a,b; pl. 135(1–3).
Assemblage (TC): Kon 222 Dic odo, Konings Kroon.
Preservation: virtually complete 'flower', part and counterpart seen from outer view, no details of inner pollen sacs visible; impression in thinly laminated, medium grey cherty shale with poor cleavage.

Reference palaeodeme—1 indiv. only (the holotype).

Specific diagnosis
A *Weltrichia* species with a broadly cup-shaped 'flower' (33 x 25 mm) and *ca* 9 deeply lobed, lanceolate microsporophylls.

Specific characters
'Flower': broadly cup-shaped (33 x 25 mm), deeply lobed around distal perimeter into *ca* 9 microsporophylls.
Microsporophyll: lanceolate (to 20 x 5 mm).

Etymology
regalis (Lat.)—royal, with reference to the type locality Konings Kroon (Afrikaans for King's Crown).

Comment & comparison
The above description is based on the single available specimen. No details of inner pollen sacs are visible.

Weltrichia helvetirara J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/22188; pl 135(4,5).
Assemblage (TC): Lit 111 Dic/Hei, Little Switzerland.
Preservation: incomplete 'flower', base, tip and some of sides missing, no counterpart, compression, some carbonised remains but mainly absent; in thinly laminated, dark grey shale with moderate cleavage.

Reference palaeodeme—1 indiv. only (the holotype).

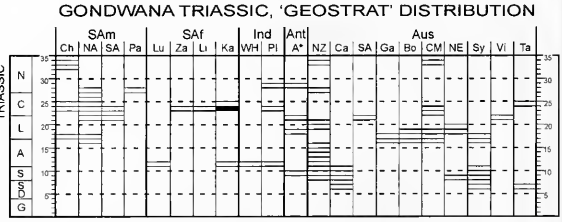
Specific diagnosis
A *Weltrichia* species with a narrowly cup-shaped 'flower' and at least 18 deeply lobed linear-lanceolate microsporophylls.

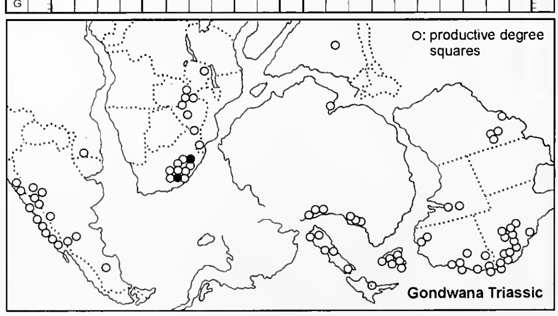
Diagnostic characters
'Flower': narrowly cup-shaped (?26 x 16 mm), deeply lobed around distal perimeter into at least 18 microsporophylls.
Microsporophyll: linear-lanceolate (up to ?10 x 2 mm).

Etymology
helvetirara—*helvetia* (Lat.), Switzerland, with reference to the type locality; *rarus* (Lat.), rare.

Comment & comparison
The description is based on the holotype alone. A possible pollen sac (tf. 2b adjacent) occurs at the inner tip of a microsporophyll, but pollen has not been extracted. A second specimen from Lit 111 [BP/2/1261, tf. 3 adjacent, pl. 135(6,7)], differs in size and relief pattern and is probably a separate species.

GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION





Cycadolepis Saporta 1873 (emend. T.M.Harris 1953)

Type species
Cycadolepis villosa Saporta 1873.
Orbagnoux, France; Triassic.

Generic characters
Dehisced bract: linear-lanceolate to arcuate, varying greatly in size (8–70 mm long), concavo-convex in transverse section, glabrous with reticulate wrinkled pattern or covered variously with hairs.

Etymology
Cycadolepis—lepis (Gr.), scale.

Global range: several spp., Pangaea, U. Tr.–U. K.

Gondwana Triassic occurrence
SAf—Karoo Basin.

Molteno occurrence
Frequency (F): 3 TCs (of 100 sampled in Molteno).
Diversity (D): 1 species.
Abundance (A): 14 indivs total; very rare to vanishingly rare.

Kon 222:	10 indivs in	40 man-hrs	(2 per 1 man-day)	very rare
Aas 411:	3 "	" 512 "	(1 " 17 ")	extremely rare
Bir 111:	1 "	" 550 "	(1 " 55 ")	vanishingly rare

Affiliated organs
Female strobilus: *Fredlindia*—Grade 3 (Mut. occ.).
Foliage: *Halleyoctenis*—Grade 3 (Kin. reinf., Mut. occ.).

Classification & comparison
Cycadolepis is generally recognised as being an individual bract from a caducous involucre enveloping hermaphroditic bennettitalean inflorescences ('flowers') such as *Williamsoniella* and *Cycadeoidea* (Menéndez 1966; Harris 1969, p.102; Watson & Sincock 1992; Stewart & Rothwell 1993, pp. 352–361).

Cycadolepis rexiplumea J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/20306a,b; pl. 136(4).
Assemblage (TC): Kon 222 Dic odo, Konings Kroon.
Preservation: virtually complete scale, part and counterpart; impression in thinly laminated, medium grey cherty shale with poor cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 10 indivs (3 complete, 2 partial, 5 isolated), pl. 136(1–7).

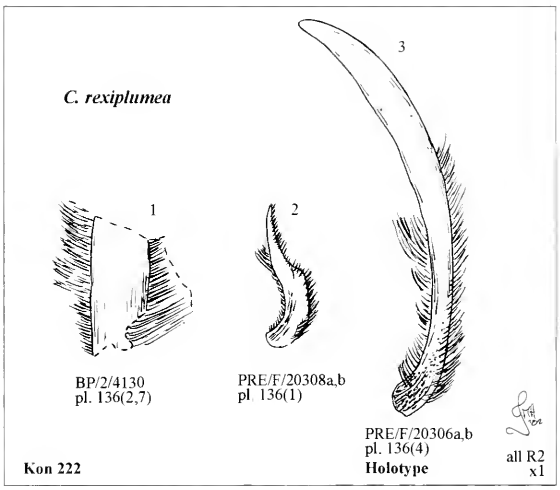
Sister palaeodemes—2 (as listed)
Aas 411: 3 indivs (1 complete, 2 partial).
Bir 111: 1 indiv. (1 complete).

Specific diagnosis
A *Cycadolepis* species with linear-lanceolate scale (20–>60 mm long), bearing numerous long abaxial hairs.

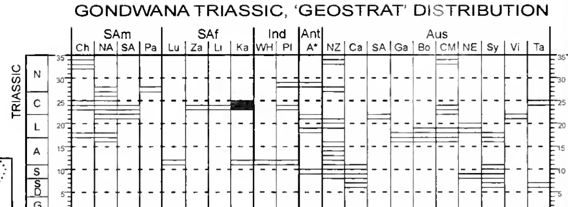
Specific characters
Scale: linear-lanceolate, of variable size (20–>60 mm long), sinuous to curved or straight; hairs abaxial, dense, of a length approaching the diameter of the scale, extending at acute angles.

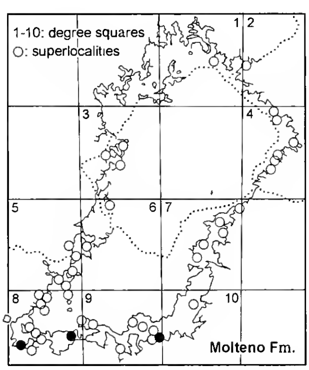
Etymology
rexiplumea—rex (Lat.), king, with reference to the type locality; *pluma* (Lat.), feather.

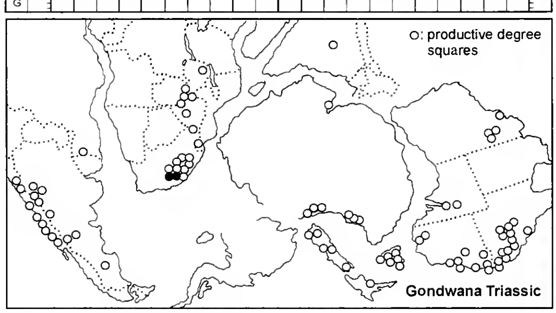
Comment & comparison
As no cuticles are known from Kon 222, close comparison with other described species cannot be made. Based on occurrence and affiliation, the Molteno material (from 3 TCs) is regarded as a new species.



GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION







Leguminanthus Kräusel & F.Schaarschm. 1966

Type species

Leguminanthus siliquosus (Leuth.) Kräusel & F.Schaarschm. 1966.
Neuewelt, Basel, Switzerland; Keuper, U. Triassic.

Generic concept

A bennettitopsid microsporangiate organ consisting of a broad oblong leaf-like pedunculate microsporophyll with laminae that are folded about a midrib and bear microsporangia arranged in rows on the inner surface.

Generic characters (Molteno Fm.)

Microsporophyll: leaf-like, broad, oblong (45 x 8 mm); peduncle short and broad; laminae folded about the broad midrib; venation parallel, lateral, at a sharp angle to the midrib; microsporangia arranged in rows and/or clusters on inner surface.
Microsporangium: minute (<0.5 mm long), irregularly round to oval.

Etymology

Leguminanthus—legumen (Lat.), bean, with reference to the leguminous pod-like appearance of the fruit.

Global range: *ca* 3 spp., Pangaea, U. Tr.

Gondwana Triassic occurrence

SAf—Karoo Basin.

Molteno occurrence

Frequency (F): 1 TC (of 100 sampled in Molteno).
Diversity (D): 1 species.
Abundance (A): 5 indivs; very rare.

Kon 222 Dic odo: 5 indivs in 40 man-hrs (1 per 1 man-day), very rare

Affiliated organs

Female strobilus: unknown.
Foliage: see relevant discussion.

Classification & comparison

Suprageneric classification (Fredlindiaceae/Fredlindiales)

Based on northern Late Triassic collections, *Leguminanthus* is considered to be a bennettitalean pollen organ (Crane 1986, 1988). Although the generic affiliation of this taxon within the Molteno is left open, it seems most likely that it falls in the family Fredlindiaceae.

Intergeneric comparison (Gondwana Triassic)

Leguminanthus is unique.

Comparison beyond Gondwana Triassic

Kräusel & Schaarschmidt (1966) made a comparison of *Leguminanthus* with other possible bennettitopsid pollen organs, e.g. *Williamsoniella, Leuthardtia, Hartingeria* and *Lunzia*, and concluded that it was unique. *Brightonia* (Harris 1932b, p. 119, pl. 19), from the Late Triassic *Lepidopteris* Zone of Greenland, was considered by Crane (1986) to be similar to *Leguminanthus*.

Reconstructions

The reconstruction (tf. 3 opposite) is based on the holotype, PRE/F/20410a,b, which shows good 3D preservation. Side 'a' clearly shows the stalk, midrib area and the two distinct sides of the lamina; side 'b', the internal cast, shows the microsporangia more clearly, and in cross section shows the incurving edge of the microsporophyll. In PRE/F/20312b, some of the microsporangia were prepared to reveal their spherical structure (tfs 1a,b opposite). The venation, as seen on the type from Switzerland, is not clearly preserved on the Molteno material and is not indicated in the drawing.

Evidence for affiliation of organs

Bennettitopsid male organs occur extremely rarely in the Molteno (Tab. 60). By far the most prolific TC, yielding all three genera recognised (*Cycadolepis, Weltrichia* and *Leguminanthus*), is Kon 222. *Cycadolepis* and *Weltrichia* are considered as affiliating with *Fredlindia.* The affiliation of the Molteno *Leguminanthus* is uncertain at present.

We provide a comparative floristic synopsis from three localities which suggests possible affiliation: the first, from the Molteno, is outlined below; the other two, from the Late Triassic of Europe, are discussed in the box at the foot of the page.

Kon 222 Dic odo, Molteno Fm.

A typical TC representing the *Dicroidium* open woodland of the floodplain. It has been well sampled, at 40 man-hours cleaving, and includes 449 catalogued slabs.

Bennettitales: This is the second most dominant gymnosperm element in the flora after *Dicroidium* (at 87%).
Foliage—1 genus, *Halleyoctenis* (8%).
Female fruit—the single new genus *Fredlindia*, with 3 individuals.
Male fruit—3 genera of apparent bennettitopsid male organs occur; *Cycadolepis, Leguminanthus* and *Weltrichia.* Apart from this Kon 222 material, *Cycadolepis* bracts are recorded from Aas 411 and Bir 111 and *Weltrichia* from Lit 111.

Various alternative interpretations concerning the nature and affiliations of these three organ-genera exist:

a) All are elements of a single complex fruit affiliated to *Fredlindia* and *Halleyoctenis.*
b) They represent three distinct organs of bennettitopsid plants, at least two of which are without female or foliage affiliates at Kon 222.
c) *Cycadolepis*, a sterile bract, pairs with either *Weltrichia* (our preference) or *Leguminanthus*, leaving at least one taxon without female or foliage affiliates. [Note that the only other possible foliage affiliate is *Pseudoctenis*, which is identified as cycad rather than bennettitopsid on the basis of gross morphology and cuticle (And. & And. 1989, pp. 280–325).]
d) One or more of these supposed male elements is not bennettitopsid.

On the bennettitopsid affiliation of *Leguminanthus* in the Late Triassic of Europe

Lunz, 100 km SW of Vienna, Austria (Carnian)

The plant beds, with several TCs over a couple of kilometres, occur within a coal-mining area which is part of a limestone sequence in the northern Alpine foothills. Marine invertebrates provide a Carnian age. Apart from the general report of Dobruskina (1988), there is no thorough documentation of abundance data per site for the Lunz collections. It is not feasible, therefore, to reliably establish affiliations based on the co-occurrence of organs at TC level. However, the flora shows a high percentage of Bennettitales (abundance and diversity), and *Leguminanthus*, with 22 individuals available, most likely affiliates with this order.

Foliage (based on the study by Dobruskina 1988):
The overall flora comprises sphenophytes (6%), ferns (7%), Bennettitales (*ca* 53%), *Taeniopteris* (17%), *Macrotaeniopteris* (<1%), ginkgophytes (13%) and conifers (5%).

Bennettitales: The dominant element of the flora, and the most diverse amongst the gymnosperm orders.
Foliage—4 species recorded: *Pterophyllum longifolium* (50%); *Pterophyllum* sp.B, *Anomozamites* sp. and *Nilssonia sturi* (each > 1%).
Female fruit—3 genera: *Westerheimia, Sturianthus, Bennetticarpus.*
Male fruit—3 genera: *Leguminanthus, Haitingeria, Cycadolepis.*

Neuewelt, Basel, Switzerland (Keuper)

Three localities, Neuewelt, Moderhalde and Hemmiken, occur within or in the neighbourhood of Basel. Neuewelt, the best known and described of the floras, comprises a number of TCs scattered around the flanks of the Rutihard hill within the city. We confine our discussion to this 'locality'. There exists no synthesis of the flora providing abundance data, so assessment of affiliations remains provisional. The link between *Leguminanthus* and a species of *Pterophyllum* seems probable.

Foliage (based on unpubl. literature survey by H.M. Anderson, 1973):
The overall flora consists of two genera and five species of sphenophyte (common to abundant), eight genera and 10 species of fern (rare to common), Bennettitales (abundant), *Taeniopteris*, ginkgophytes (common) and conifers (? rare).

Bennettitales: The dominant gymnospermous element in the flora.
Foliage—1 genus: *Pterophyllum* (3 recorded species); the second most abundant element in the flora after *Equisetum.*
Female fruit—unknown.
Male fruit—2 genera: *Leguminanthus* (*ca* 3 indivs); *Williamsonianthus keuperianthus* (based on a single specimen with 6 cupules).

Leguminanthus leopardus J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/20410a,b; pls 137(3–5), 138(3–5).
Assemblage (TC): Kon 222 Dic odo, Konings Kroon.
Preservation: a complete specimen, part and counterpart, longitudinal view; 3D mould and cast in thinly laminated, medium grey cherty shale with poor cleavage.

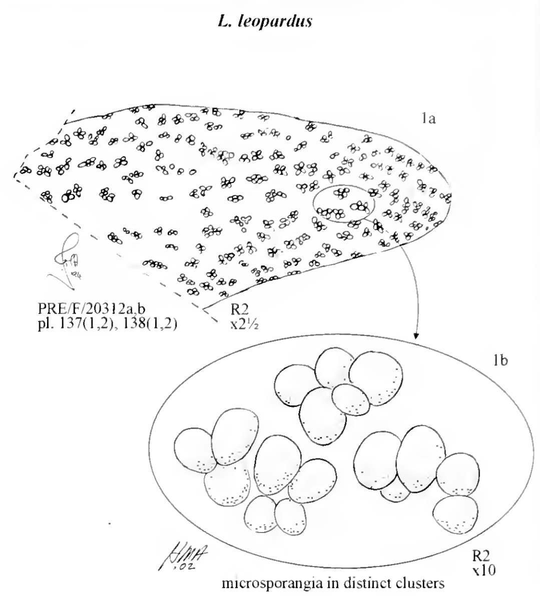
Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 5 indivs (3 intact, 1 partial, 1 isolated), pls 137, 138.

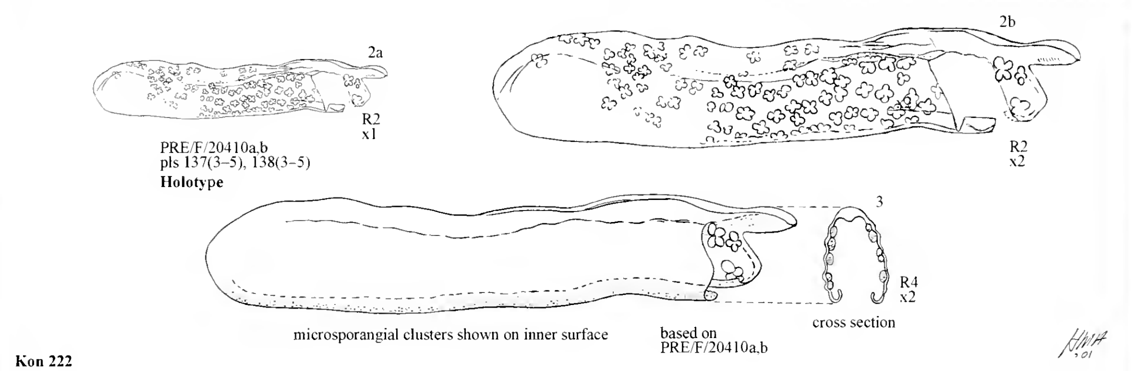
Specific diagnosis
A *Leguminanthus* species with clusters of circular to oval microsporangia aligned in irregular diagonal to horizontal rows.

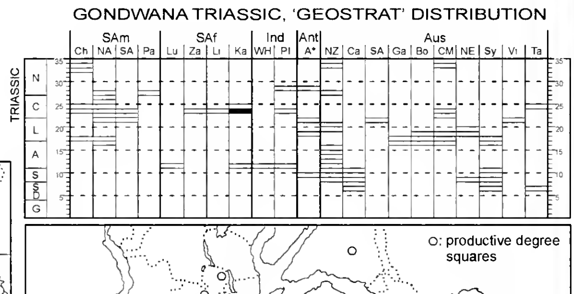
Specific characters (Molteno Fm.)—as for genus.

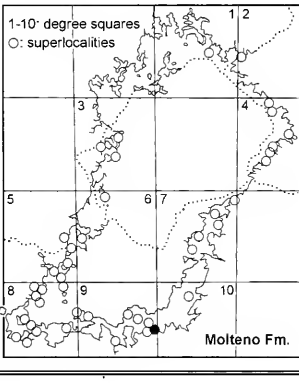
Etymology
leopardus (Lat.)—leopard, with reference to the appearance of the microsporangial groups (particularly in the unprepared specimens), reminiscent of the markings of a leopard.

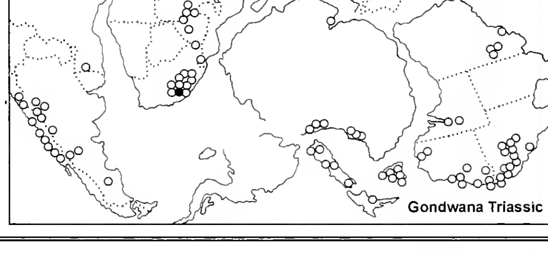
Comment & comparison
The Molteno specimens closely resemble the type species in general morphology, but differ in the arrangement of the putative microsporangia into irregular diagonally aligned clusters rather than in clear transverse rows.











Halleyoctenis J.M.And. & H.M.And. 1989

Type species
Halleyoctenis multilineata (Shirley 1897) J.M.And. & H.M.And. 1989.
Ipswich-Esk, Clarence-Moreton Basin, Queensland; Carnian, Triassic.

Generic diagnosis
A bennettitopsid leaf with roundly truncate pinnae and fine, very closely spaced, parallel, occasionally forking venation.

Generic characters (based on the three definite Gondwana species)
Leaf: small to large, obovate to narrowly elliptic, simply pinnate; pinnae laterally to slightly dorsally attached, margins entire, oblong to narrowly oblong, apex truncate, base slightly expanded or contracted; veins numerous, very closely spaced, parallel, occasionally forking but not anastomosing, terminating along the pinna margin and mostly across apex.
Cuticle: see And. & And. (1989, p. 327); this vol., tfs 1–3 adjacent.

Eponymy
Halleyoctenis—after the English astronomer E. Halley, and the cycad leaf *Ctenis*.

Global range: 3 spp., Gondwana, M.–U. Tr. (ANS–CRN).
First: *Halleyoctenis* sp. (Webb 1980); UQL.4224, Bryden Fm., Ipswich/Esk, Australia.
Last: *H. brachypinnata*, Molteno Fm.

Gondwana Triassic occurrence
Frequency (F): 7 degree squares (of the 84 across Gondwana).
Ubiquity (U): 2 continents (of 5 comprising Gondwana).
Diversity (D): 3 foliage species.
Abundance (A): 2% (the norm as in Molteno TCs).
Longevity (L): 9 myrs (late Anisian to Lower Carnian).

Colonisation success: FUDAL rating 7/2/3/2/9 = 24.
Limited success (Grade 2): *Halleyoctenis* was the 14th most prominent foliage genus in the Gondwana Triassic; it enjoyed relatively low to moderate frequency, ubiquity, diversity, abundance and longevity.
Endemism: of the 3 (+1; see Umk 111, BP/2/793, tfs 5, 6 opposite) described Gondwana Triassic species, 2 are basin endemics and 2 are single-assemblage endemics.

Molteno occurrence
Frequency (F): 10 TCs (of 100 sampled in the Molteno).
Diversity (D): 2 (+1; see Umk 111, BP/2/793, tfs 5, 6 opposite) species.
Abundance (A): abundant (8–15%) in 2 TCs; rare to extremely rare (<1%) in 8 TCs.

Habit: probably cycad-like plants.
Preferred habitat: most common in *Dicroidium* open woodland, more rare in closed woodland of the lake margin.

Affiliated organs
Female strobilus: *Fredlindia*—Grade 3 (Mut. occ.).
Male strobilus: *Cycadolepis*/*Weltrichia*—Grade 3 (Mut. occ., Kin. reinf.).

Classification & comparison
Suprageneric classification
In many of its features, *Halleyoctenis* is the perfect proto-bennettitalean foliage. It has more in common with a number of the early members of the Bennettitales as known from the Late Triassic of the northern hemisphere than with the more typical forms of the Jurassic (e.g. Harris 1969).

Intergeneric comparison
Laurozamites Weber & Zamudio-Varela (1995) is the most common element of the Late Triassic (Carnian) Santa Clara Fm. of Sonora, Mexico. It has been collected from many localities and several species are recognised. *Zamites powelli*, now included in *Laurozamites* (Weber & Zamudio-Varela 1995), is one of the most common leaves (from about 35 localities) in the Carnian to Lower Norian formations of the Late Triassic in the USA (Ash 1975). *Laurozamites* is very like *Halleyoctenis* in the general appearance of the frond, in the shape of the pinnae with their truncate apex, in the very fine closely spaced, parallel to slightly spreading venation, and in several features of the cuticle, such as the transverse stomata, the guard cells, the shape of the cells both veinal and interveinal, and the single papilla per cell. It is more bennettitalean than *Halleyoctenis* in the strongly contracted base of the pinnae and their marked dorsal attachment, and in critically diagnostic features of the cuticle such as the mildly sinuous to meandering cell walls, the pair of well-differentiated subsidiary cells and the greater stomatal frequency.

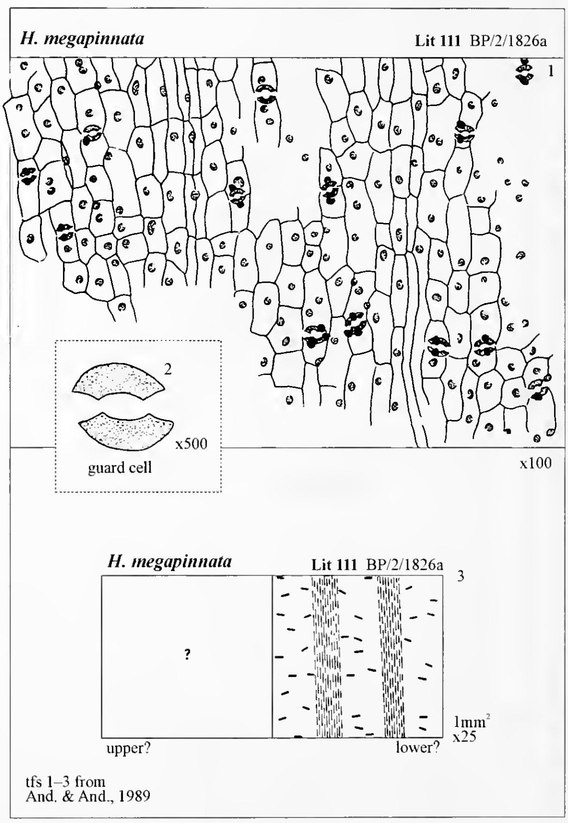
Certain Late Triassic species of the bennettitalean genus *Pterophyllum* also have much in common with *Halleyoctenis*. Examples include *P. aequale* from the Donetz Basin, Russia (Stanislavsky 1976), and *P.* spp. from the Hunan Province, China (Zhou Zhiyan 1989). These bear oblong pinnae with truncate apices and appear, at least partly, to be laterally attached and are not contracted at the base. They differ from *Halleyoctenis* in their more widely spaced veins. The cuticle of the Chinese species, with oblong cells and transverse stomata, although with greater stomatal frequency and mildly meandering cell walls, is similar to that of *Laurozamites* and is transitional between *Halleyoctenis* and the Jurassic Bennettitales.

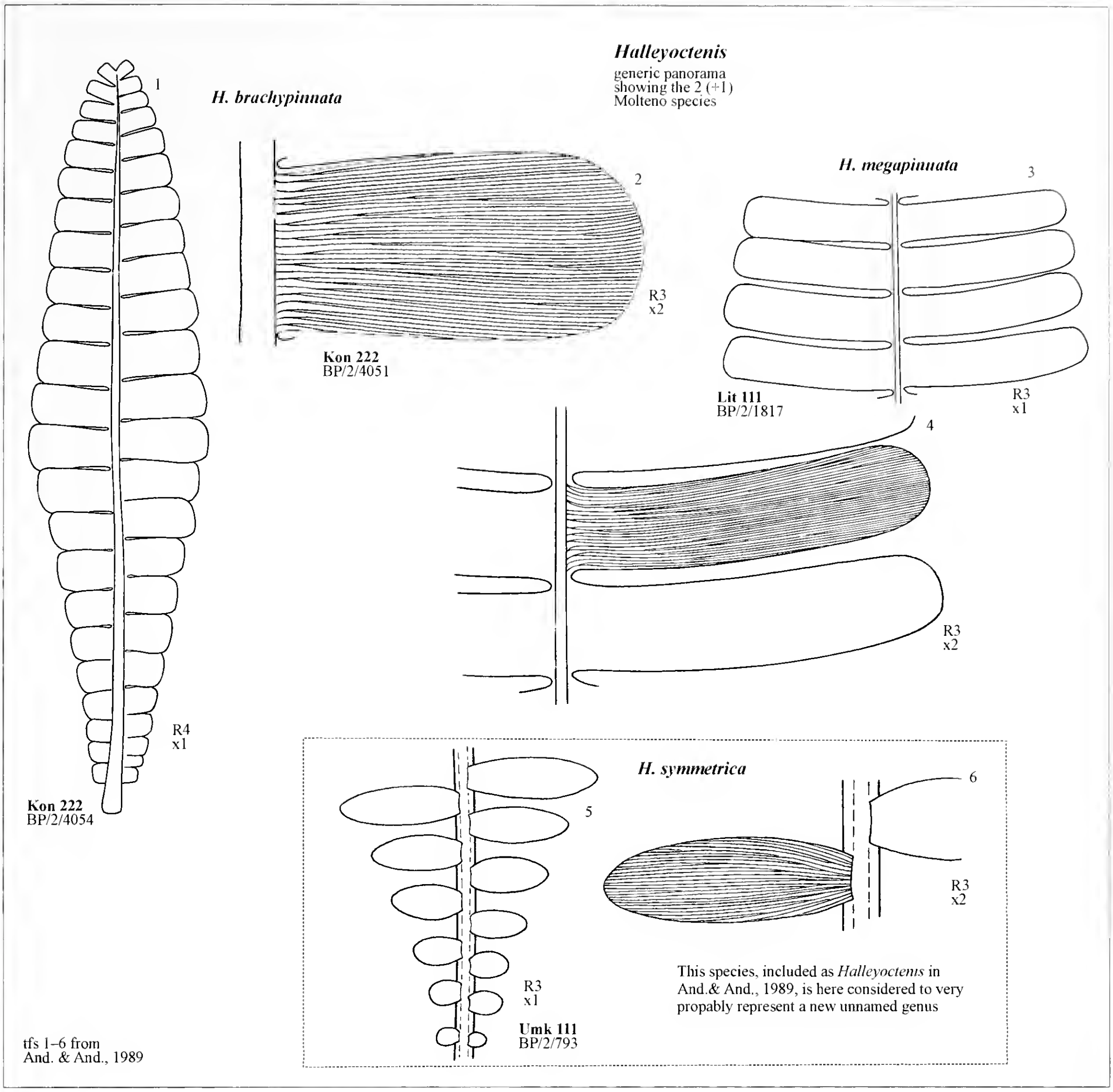
Based on both mega- and micromorphological characters, *Halleyoctenis* is readily differentiated from the four Gondwana Triassic cycad genera. It is perhaps nearest to *Pseudoctenis* in frond morphology, but differs most notably in the transverse orientation of the stomata.

Interspecific comparison
Four species are recognised in the Gondwana Triassic (And. & And. 1989). The two Molteno species, *H. brachypinnata* and *H. megapinnata*, and the Australian species *H. multilineata* are closely similar—their distinguishing features being the shape and size of the frond and the individual pinnae. Cuticle is known only for *H. megapinnata*. The single specimen from Umk 111 (BP/2/793, tfs 5, 6 opposite), described in our earlier work as *H. symmetrica*, should very probably be transferred to a new genus.

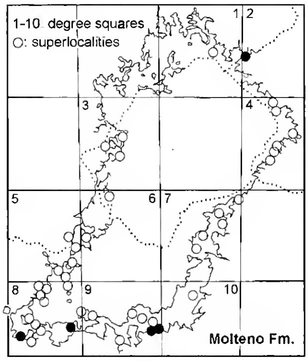
The Molteno collections of *Halleyoctenis* have at least doubled (Tab. 60) in assemblages (five new TCs) and individuals since our original description of the genus (And. & And. 1989), and an updated systematic comparative study of the full set of palaeodemes is due.

Herbst & Troncoso (2000) describe two specimens as *Pseudoctenis multilineatum* from locality 274, near Copiapó, La Ternera Fm., Chile. Their illustrated specimen showed a small frond fragment with venation that we consider insufficiently preserved to verify their identification. Herbst & Troncoso have not accepted our transfer (And. & And. 1989) of *Pterophyllum multilineata* Shirley to the bennettitalean genus *Halleyoctenis*, although that decision was based on good cuticular evidence from the Molteno. Instead, they place their specimen, without preserved cuticle in support, in the cycad genus *Pseudoctenis*.

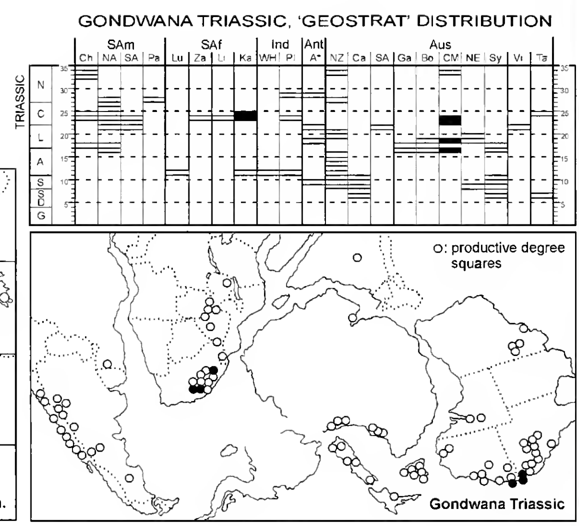




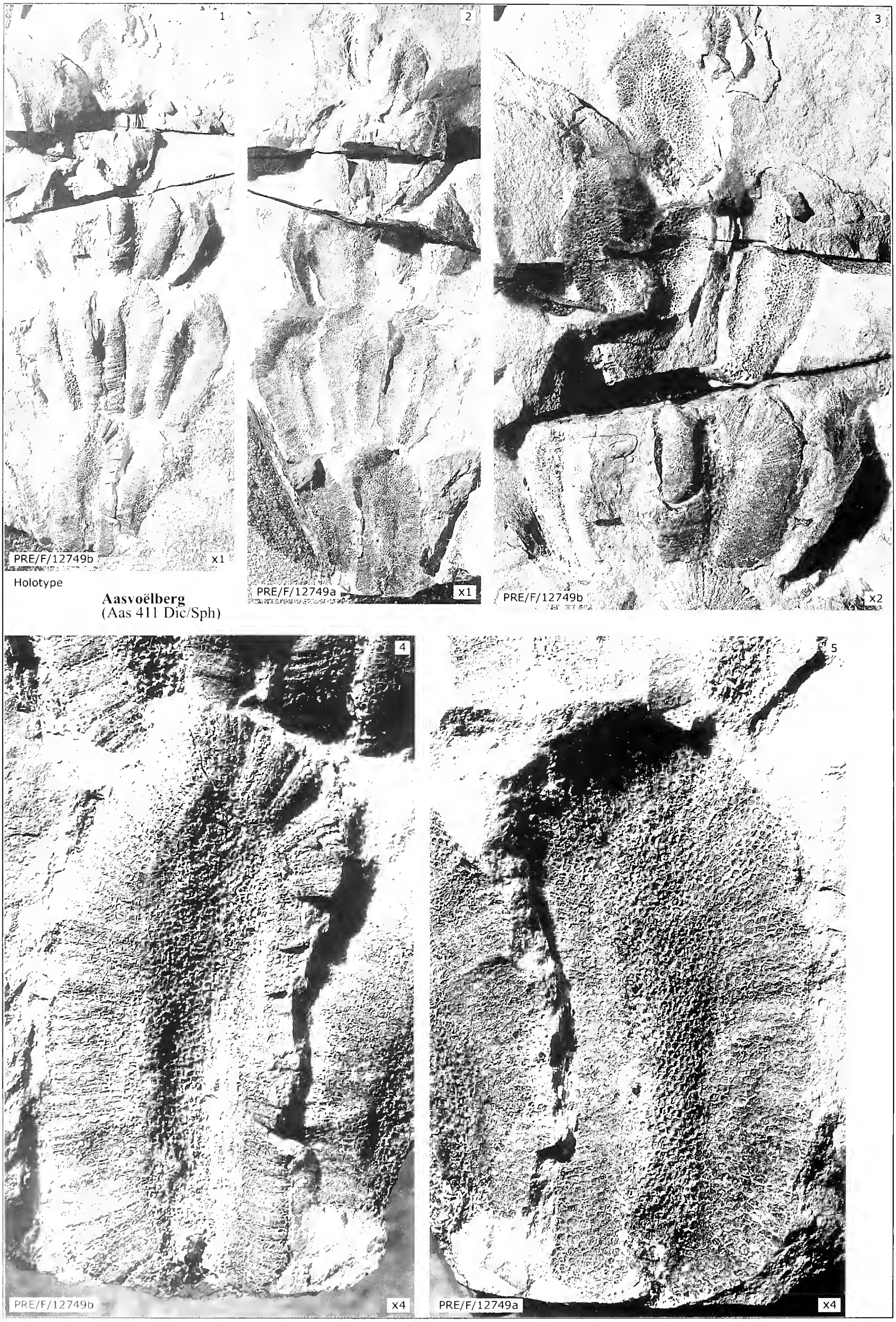
Halleyoctenis
generic panorama showing the 2 (+1) Molteno species
H. brachypinnata
1
Kon 222
BP/2/4054
R4
x1
2
Kon 222
BP/2/4051
R3
x2
H. megapinnata
3
Lit 111
BP/2/1817
R3
x1
4
R3
x2
H. symmetrica
5
R3
x1
Umk 111
BP/2/793
6
R3
x2
This species, included as *Halleyoctenis* in And.& And., 1989, is here considered to very propably represent a new unnamed genus
tfs 1–6 from And. & And., 1989

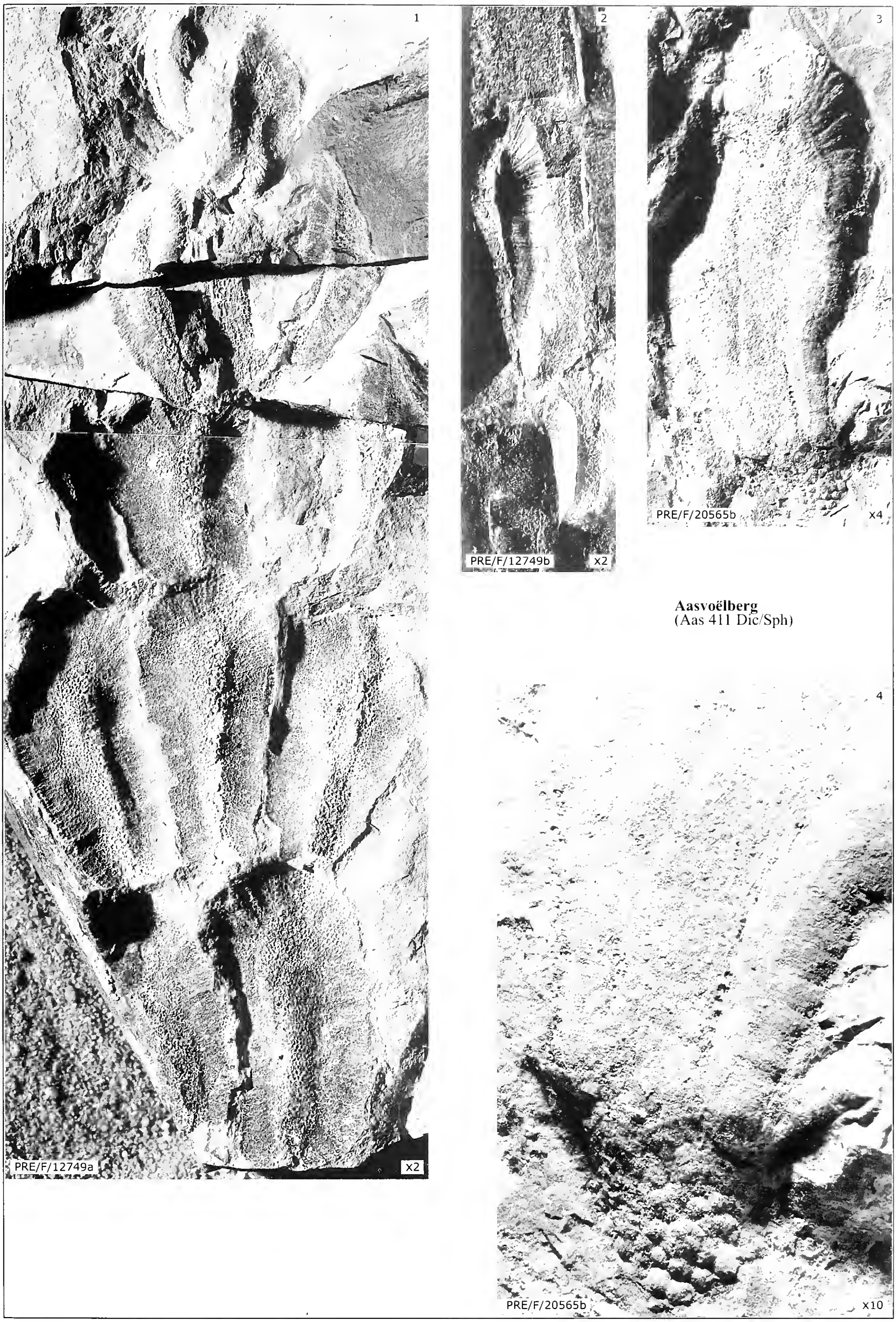


1-10 degree squares
○: superlocalities
Molteno Fm.

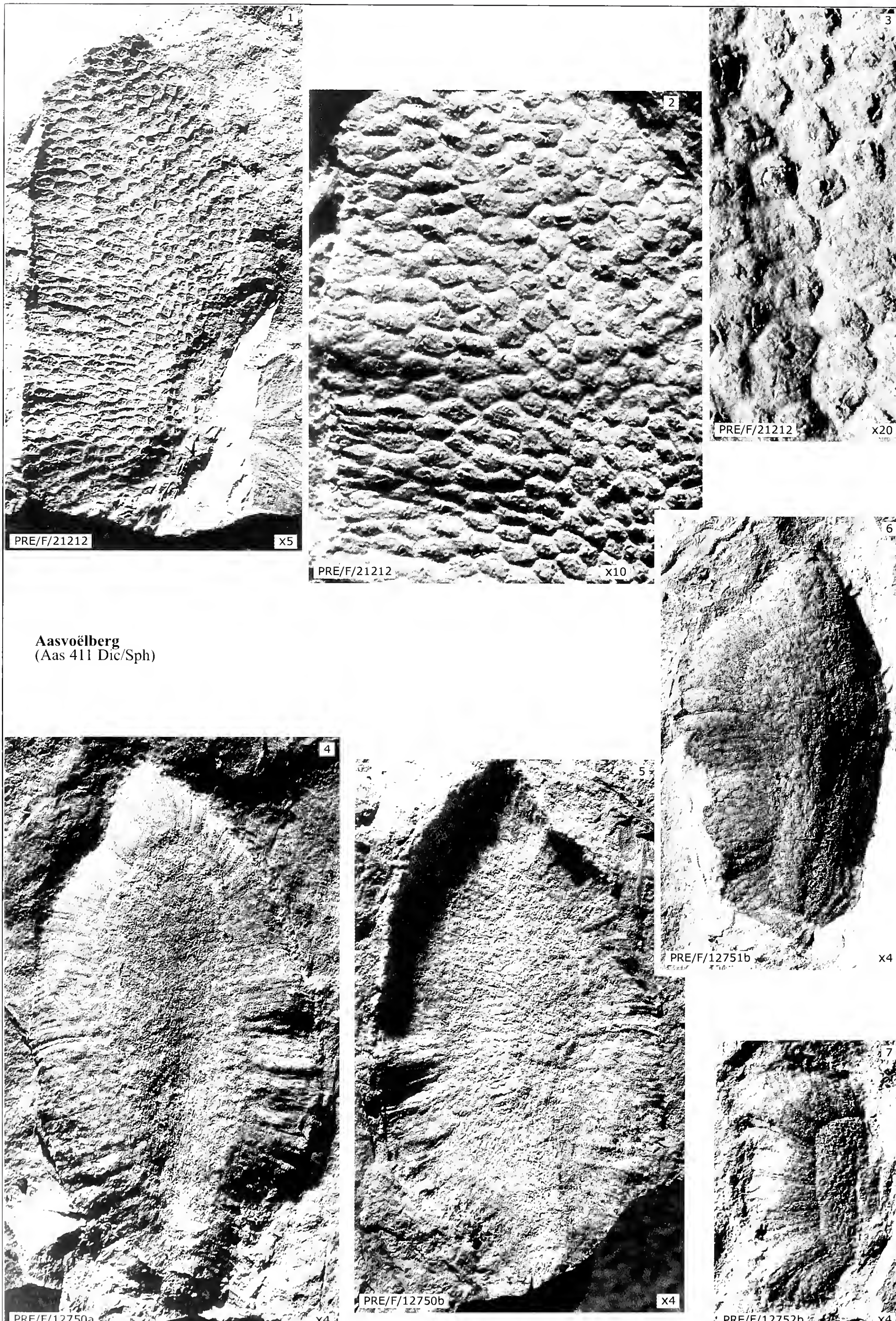


GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION
SAm
SAf
Ind
Ant
Aus
TRIASSIC
○: productive degree squares
Gondwana Triassic


1
2
3
PRE/F/12749b
x1
Holotype
PRE/F/12749a
x1
Aasvoëlberg
(Aas 411 Dic/Sph)
PRE/F/12749b
x2
4
5
PRE/F/12749b
x4
PRE/F/12749a
x4



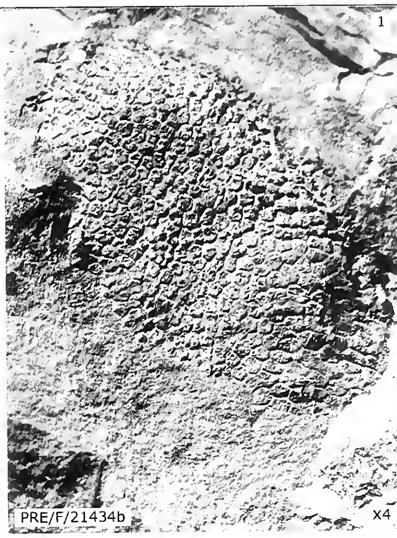
Aasvoëlberg
(Aas 411 Dic/Sph)

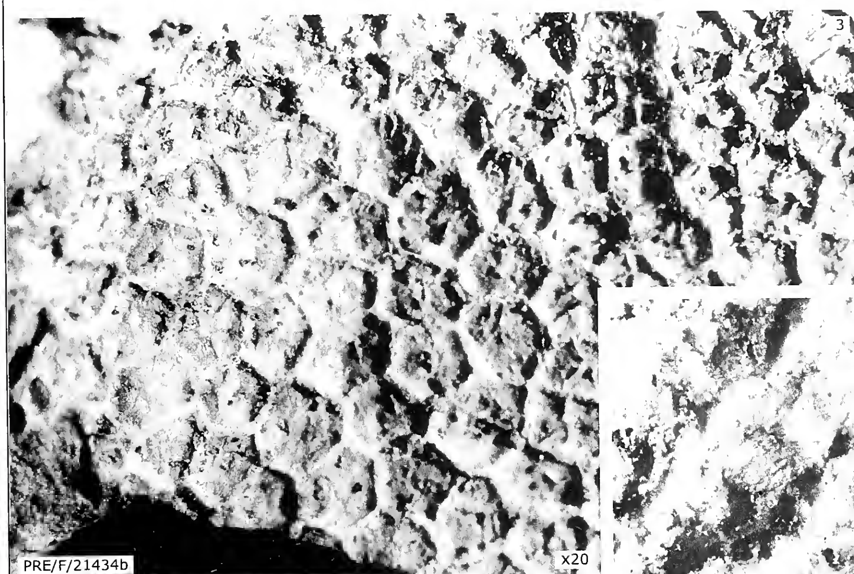


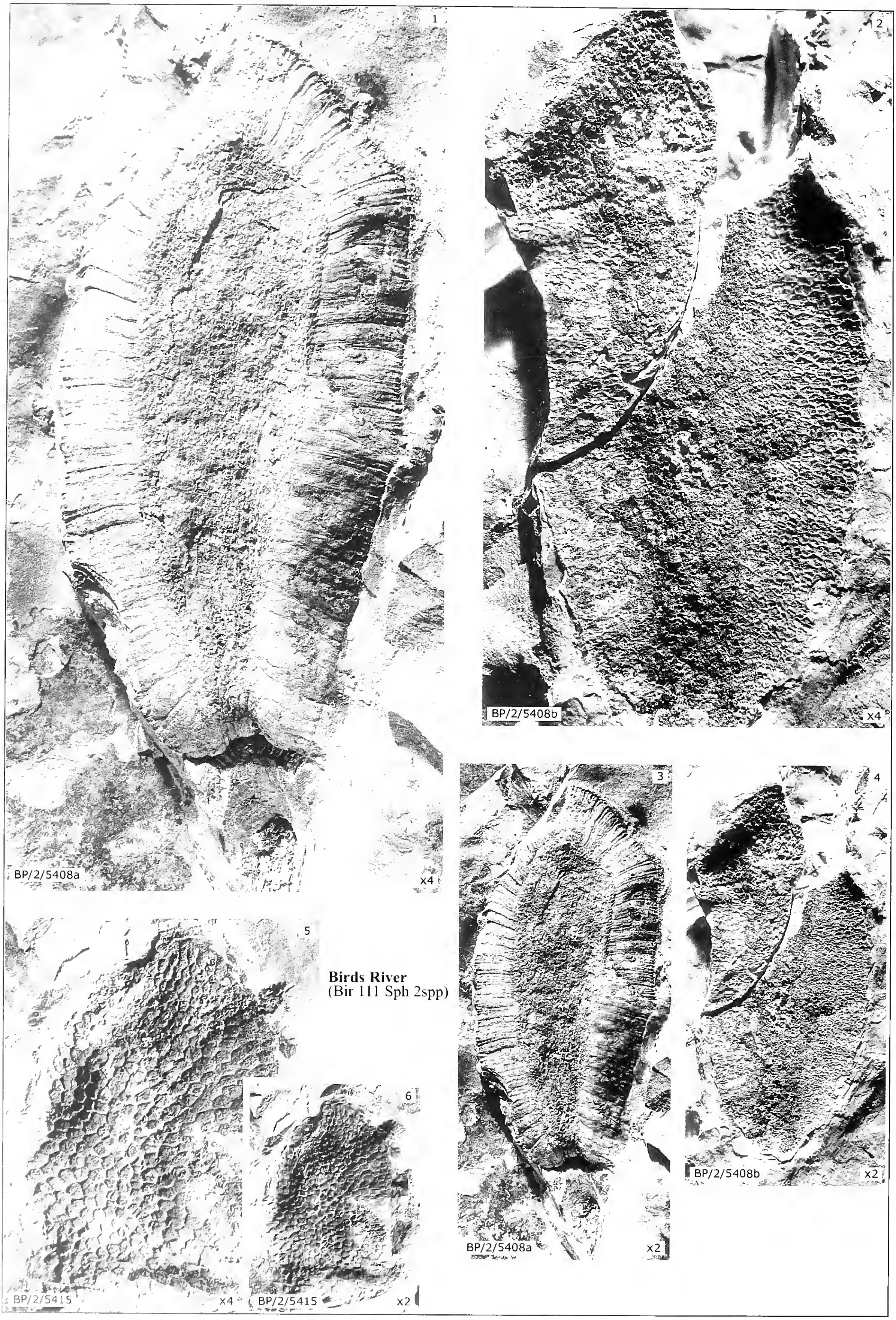
Aasvoëlberg
(Aas 411 Dic/Sph)

Fredlindia fontifructus **pl. 131** **FREDLINDIALES**

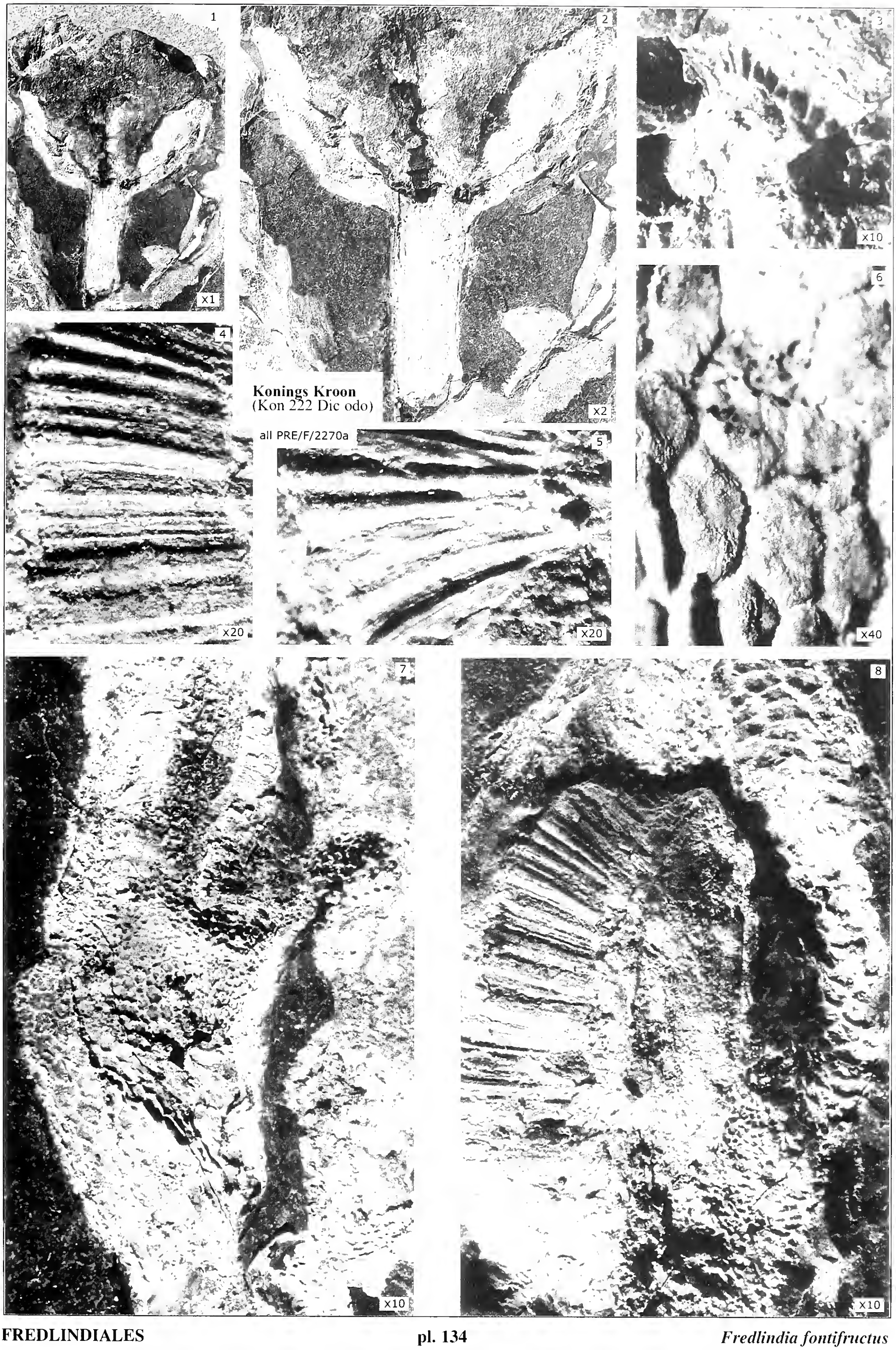
Aasvoëlberg
(Aas 411 Dic/Sph)

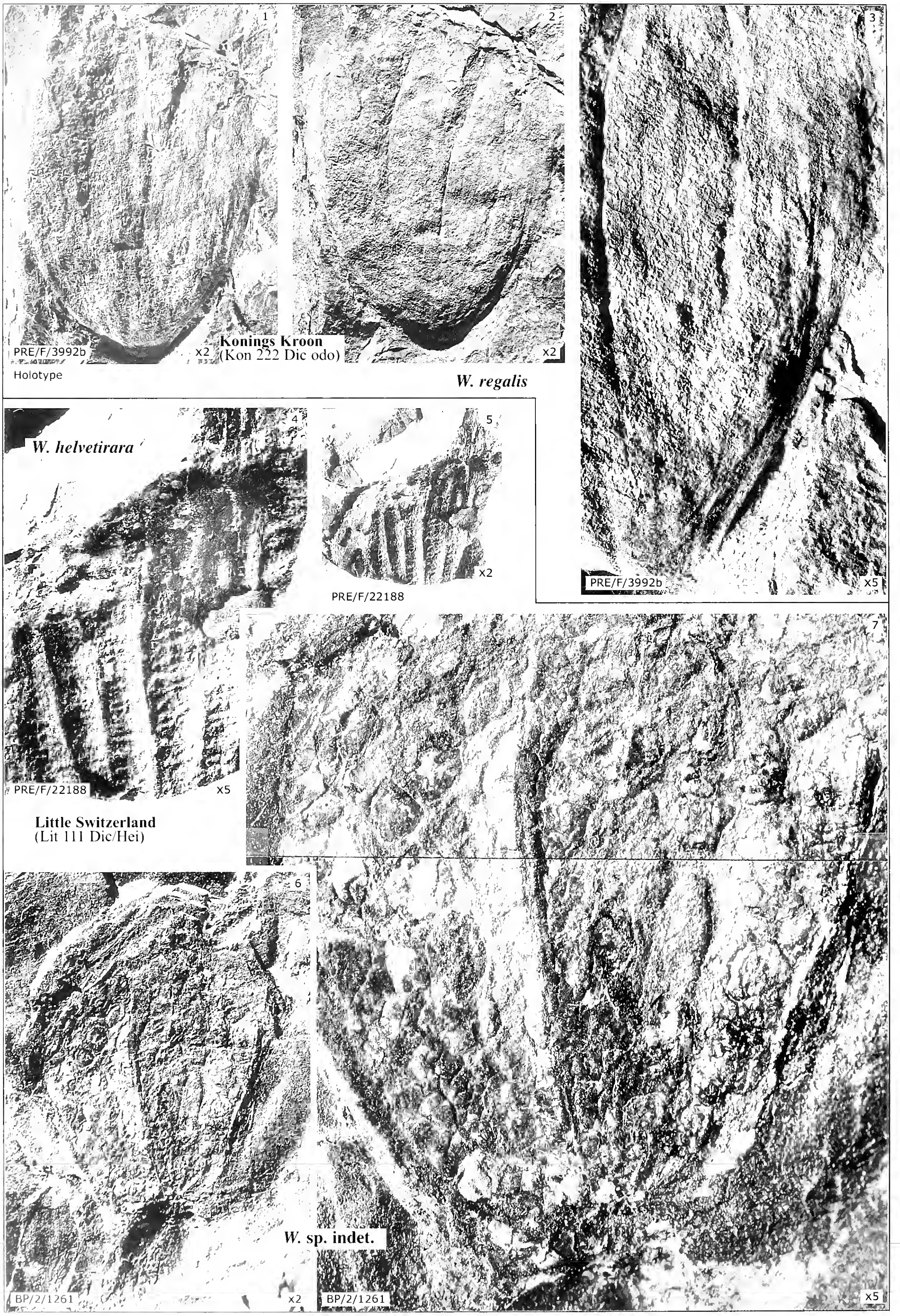


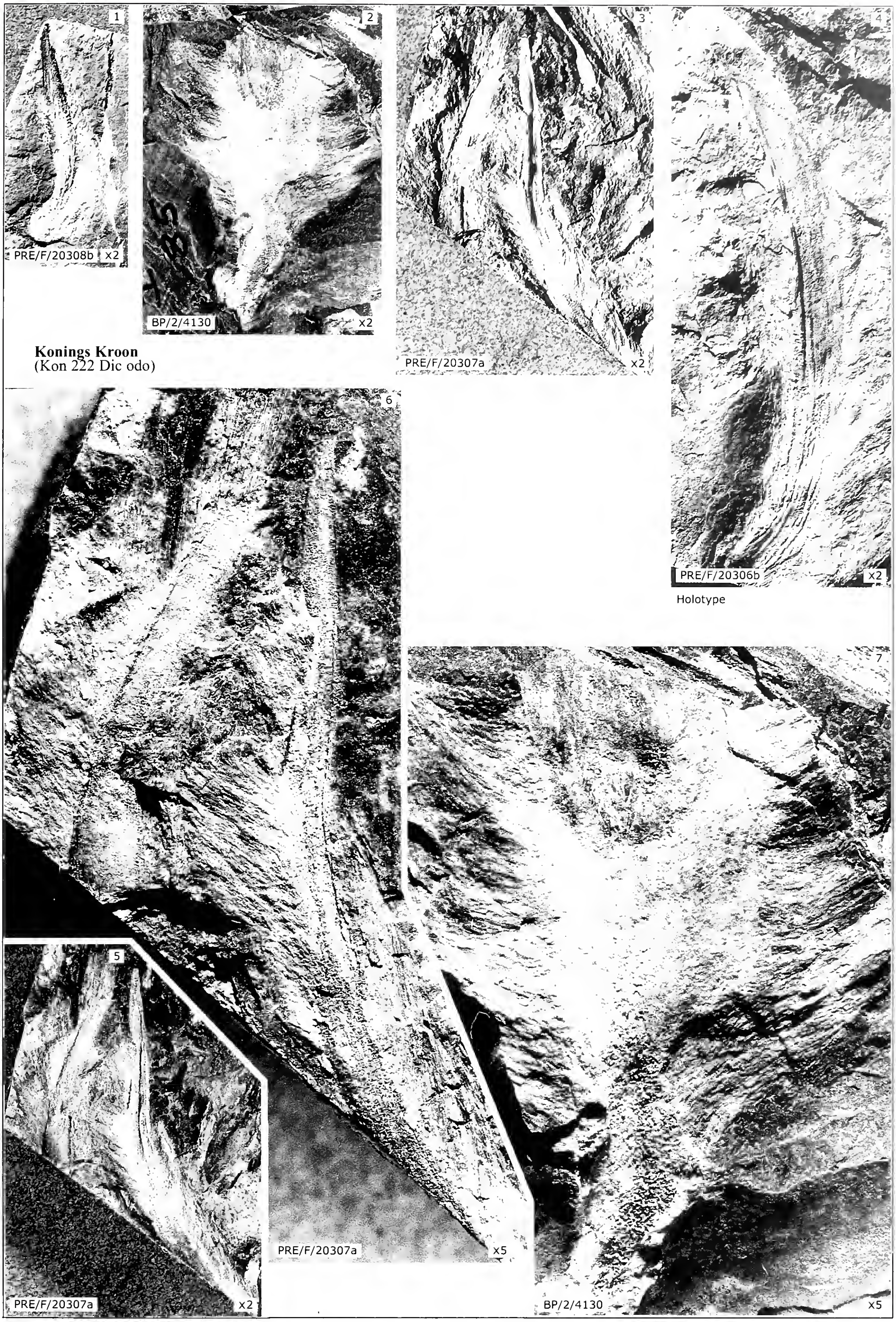




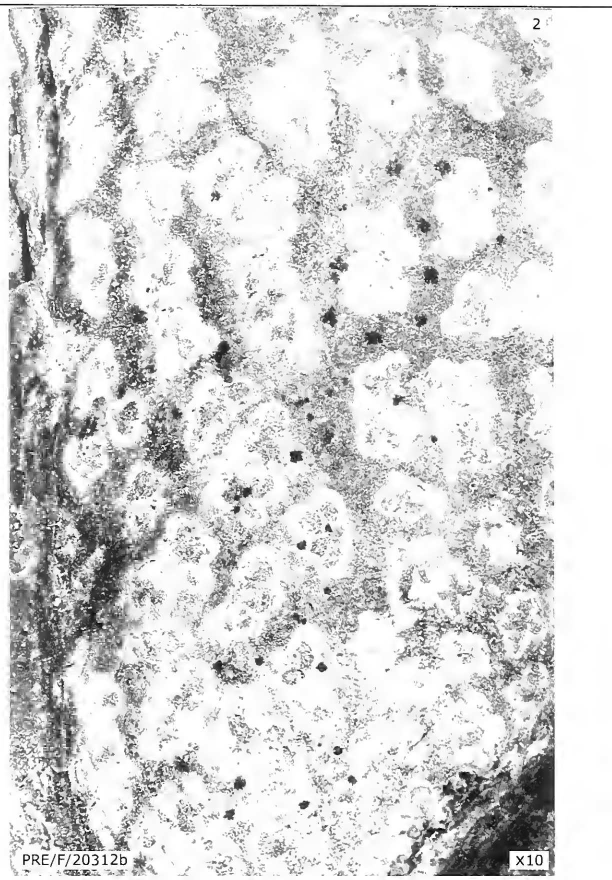
Fredlindia fontifructus **pl. 133** **FREDLINDIALES**


1
x1
2
x2
3
x10
4
x20
Konings Kroon
(Kon 222 Dic odo)
all PRE/F/2270a
5
x20
6
x40
7
x10
8
x10

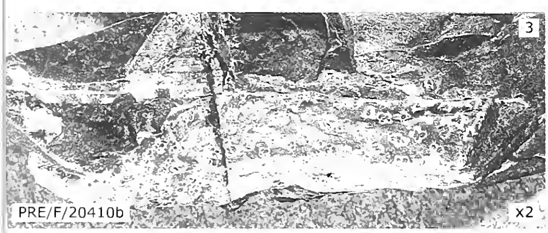

1
PRE/F/3992b
x2
Holotype
2
Konings Kroon
(Kon 222 Dic odo)
x2
W. regalis
3
PRE/F/3992b
x5
4
W. helvetirara
PRE/F/22188
x5
5
x2
PRE/F/22188
Little Switzerland
(Lit 111 Dic/Hei)
7
6
W. sp. indet.
BP/2/1261
x2
BP/2/1261
x5



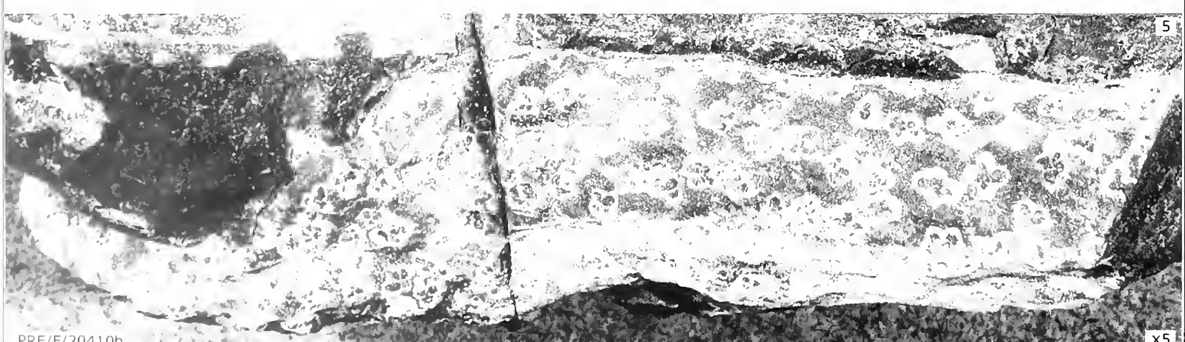
FREDLINDIALES **pl. 136** ***Cycadolepis rexiplumea***

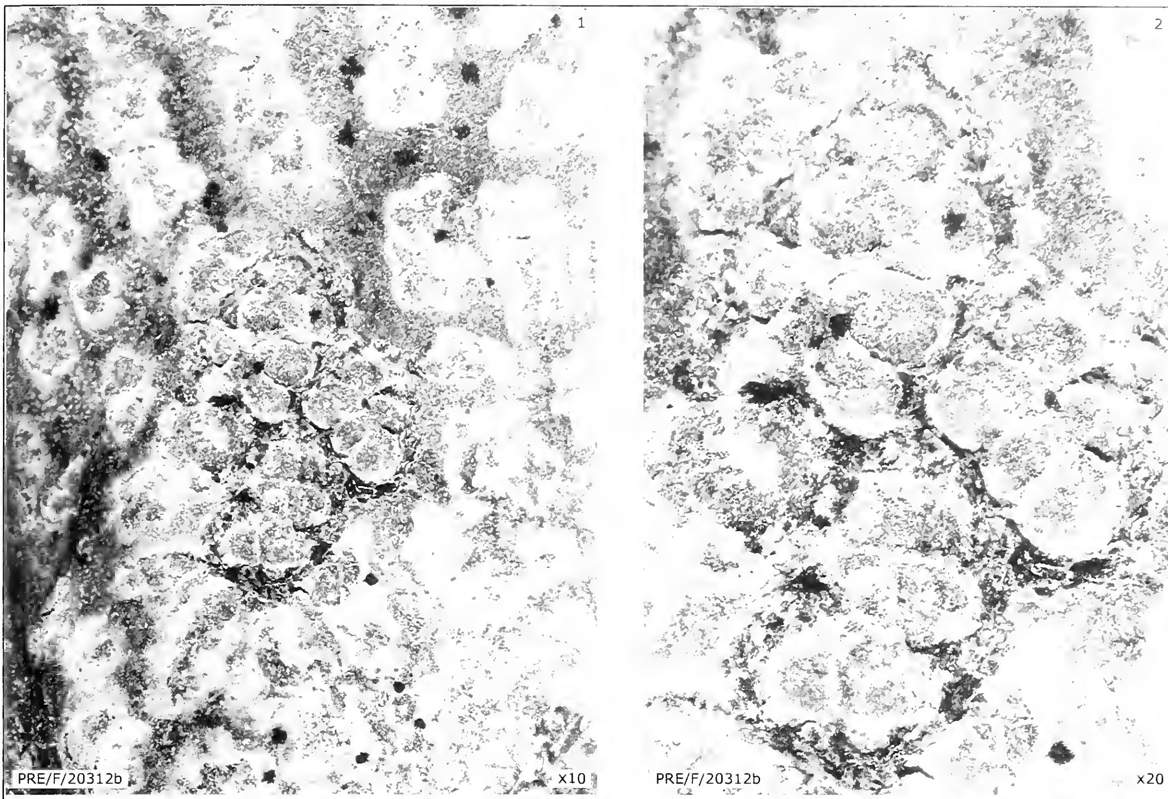


Konings Kroon
(Kon 222 Dic odo)

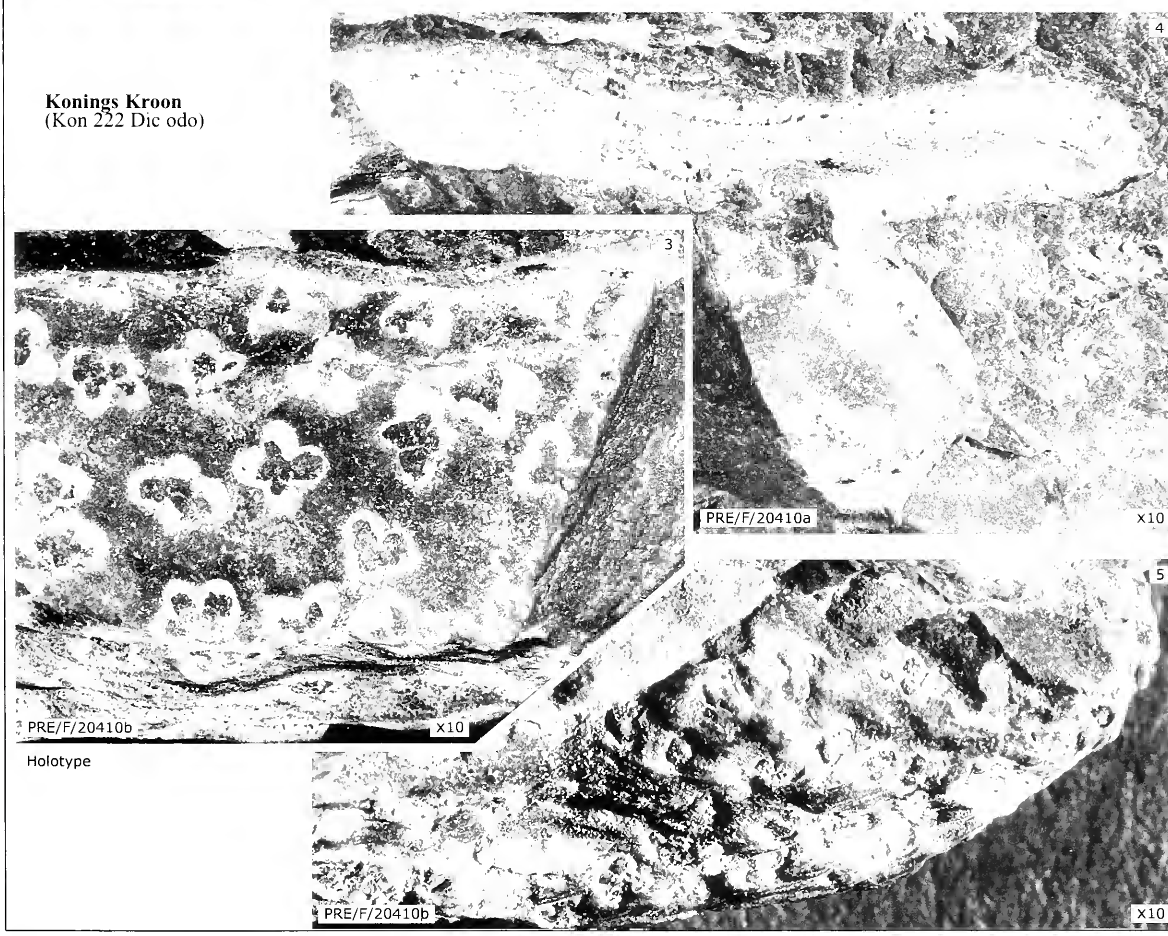


Holotype





Konings Kroon
(Kon 222 Dic odo)



Holotype

BENNETTITOPSIDA

PENTOXYLALES Pilg. & Melch. 1954

LINDTHECACEAE J.M.And. & H.M.And., fam. nov.

Lindtheca J.M.And. & H.M.And., gen. nov.

Type species
Lindtheca hackysackia J.M.And. & H.M.And., sp. nov.
Aasvoëlberg, Karoo Formation, S. Africa, Carnian, Triassic.

Generic diagnosis
A pentoxylalean ovulate structure comprising a spherical 'gynoecium' with 15–20 ovuliferous 'cells' (megasporophylls) each containing 5 ovules.

Generic characters
Strobilus: unknown
'Gynoecium': radially symmetrical, spherical pedunculate balls, apparently succulent, small (*ca* 10 mm diam.); with an aggregate of 15–20 pentagonal segments or ovuliferous cells (megasporophylls); an outer 'skin', with well-defined puckered sutures that follow the pentagonal outlines of each segment, covers the 'gynoecium'; peduncle known only through clear attachment scar, evidently gracile.
Ovuliferous 'cell': prism-shaped, radiating from a central receptacle, irregularly pentagonal in section; multi-ovulate, apparently with 5 seminal scales per 'cell' each bearing an ovule; micropyle distinct, circular, off-centre, with a clear pattern of radiating cells on outer skin.

Eponymy
Lindtheca—in honour of Linda Terblanche, on whose farm the type locality Aasvoëlberg (Aas 411) occurs.

Global range: 1 sp., Gondwana, Tr. (CRN).
First & last: Molteno Fm.

Gondwana Triassic occurrence
SAf—Karoo Basin, 1 TC (16 indivs).

Molteno occurrence
Frequency (F): 1 TC (of 100 sampled in the Molteno).
Diversity (D): 1 species.
Abundance (A): 16 indivs; very rare.
Aas 411 Dic/Sph: 16 indivs in 512 man-hrs (1 per 4 man-days) very rare

Affiliated organs
Male strobilus: unknown.
Foliage: *Taeniopteris homerifolius*—Grade 3 (Kin. reinf., Mut. occ.).

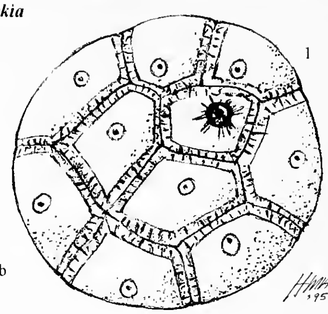
Classification & comparison
Suprageneric classification (Lindthecaceae/Pentoxylales)
The pentoxylalean ovulate genus *Carnoconites* (Crane 1985) is widely known in the Jurassic and Lower Cretaceous of India (Bose *et al.* 1985), Australia (White 1981; Drinnan & Chambers 1985) and New Zealand (Harris 1962, 1982). *Carnoconites* is a unique fructification, which has spherical 'gynoecia' with numerous uni-ovulate 'cells'. *Lindtheca* is similar to *Carnoconites* in all features with the exception that it is multi-ovulate. On this basis we place *Lindtheca* in the order Pentoxylales and in the new family Lindthecaceae. *Lindtheca* is the first genus allied to *Carnoconites* to be described from the Triassic.

Intergeneric comparison (Gondwana Triassic)
Lindtheca is unique.

Evidence for affiliation of organs
Kindred reinforcement
Nipaniophyllum is a *Taeniopteris*-like leaf that has been affiliated with cones and stems and placed in the order Pentoxylales (Sahni 1948; Stewart & Rothwell 1993). *Lindtheca*, placed in the Pentoxylales, is thus more likely to be affiliated with a *Taeniopteris*-like leaf.

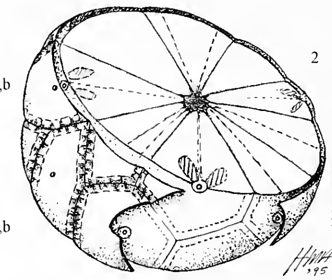
Mutual occurrence
The 16 individuals of *Lindtheca*—all isolated 'gynoecia'—derive from a single TC, Aas 411. Of all the gymnosperm foliage genera found at Aas 411, *Taeniopteris* is the most likely affiliate. All other gymnosperm leaf genera have been assigned affiliates except for a *Pseudoctenis* species here classified as a cycad. Cuticle, not preserved at Aas 411, is unavailable to confirm affiliations.

L. hackysackia



based on
PRE/F/21431a,b
pl. 139(1–6)

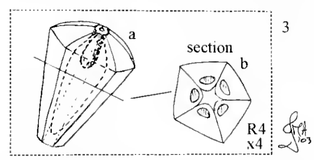
External view of reconstructed "gynoecium"
with clearly demarkated quilted segments, off-centre micropyle seen on the enclosing bladder; and the scar marking the attachment of the gracile peduncle



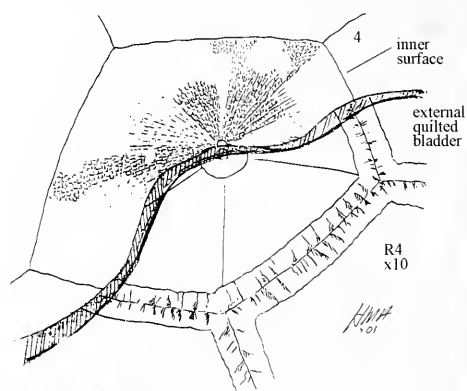
outer bladder
based on
PRE/F/21431a,b
pl. 139(1–6)

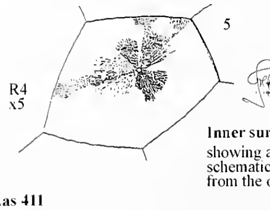
inner surface
based on
PRE/F/21140a,b
pl. 140(1–4)

Equatorial cross-section of "gynoecium"
emphasizing the well-developed, free, quilted bladder; and our favoured interpretation of the internal structure with receptacle, radiating ovuliferous segments ("cells") and seeds



Isolated ovuliferous "cell"
showing our preferred interpretation of seed emplacement; a second option would be for the seed to be reversed and emplaced at the narrow end of the "cell".





Inner surface view of bladder
showing a single pentagonal segment with schematic representation of cells radiating out from the off-centre micropyle

Aas 411

Reconstructions

'Gynoecium'

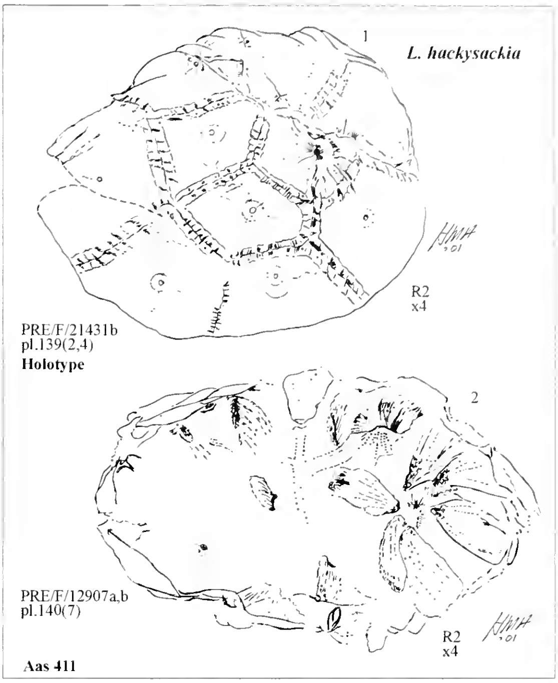
Only two specimens are preserved in external view. It is possible that these are immature fruit retaining a tough protective outer skin. The holotype shows a clear peduncle scar *ca* 1 mm in diameter. It is probable that *Lindtheca* gynoecia occurred in a compound strobilus similar to that of *Carnoconites*.

The external architecture of the quilted, hackysacky-like, ovulate 'gynoecium', tf. 1 opposite, is based on the clearly preserved holotype (PRE/F/21431a,b). A second specimen [PRE/F/21140a,b, pl. 140(1–4)] shows an inner view with the cell outlines preserved, but not the sutured quilting. The internal organisation is based on information from most of the remaining specimens. PRE/F/21432a,b, pl. 140(5, 6), shows numerous (*ca* 75) ovules (the darker ellipsoidal shapes), some of which are grouped around a central cavity.

Ovuliferous 'cell'

The ovules are interpreted to be in groups of five. This is supported by the total number of ovules being *ca* 75 and the outer polygonal areas numbering *ca* 15 (15 segments or 'cells' with five ovules each). The position of the ovules is inferred from specimens PRE/F/12907, pl. 140(7), PRE/F/21079 and PRE/F/21080a,b. In these cross section views the ovuliferous 'cells' (prism segments) are seen as triangular wedges with a darker area at the narrow end towards the central receptacle area.

A problem with this interpretation is that the ovules are not all found near the inferred core area. It is possible that they became spread out when squashed prior to or during fossilisation.



Lindtheca hackysackia J.M.And. & H.M.And., sp. nov.

Holotype

Specimen: PRE/F/21431a,b; pl. 139(1–6).

Assemblage (TC): Aas 411 Dic/Sph, Aasvoëlberg.

Preservation: complete 'gynoecium', clearly showing the outer architecture and fine cellular details, part and counterpart; impression in thinly laminated, strongly baked, yellowish grey shale with very good cleavage.

Reference palaeodeme

Assemblage (TC): as for holotype.

Specimens: 16 individuals; all detached (without peduncle), variously complete and squashed 'gynoecia'; the holotype and one other fragment show the head in outer aspect, while the remaining 14 specimens expose inner views of the structure with its numerous ovules (pls 139, 140).

Specific diagnosis—as for genus.

Specific characters—as for genus.

Etymology

hackysackia—with reference to the small, leathery, hackysacky ball (used in a USA ball game) to which the ovulate 'gynoecium' of this species bears a striking resemblance.

Comment & comparison—as for genus.

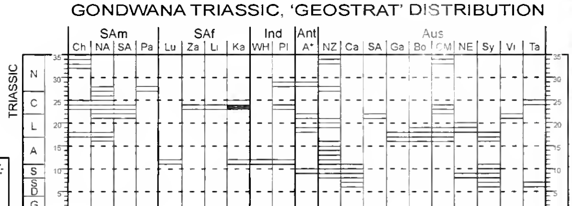
Male pentoxylalean strobili

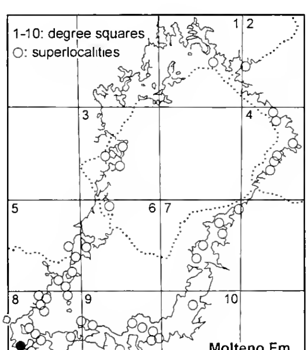
Sahnia (Lower Cretaceous, Rajmahal Hills, India), the male pentoxylalean strobilus, is branched and bears pedicellate spherical (*ca* 0.4 mm diam.) microsporangia; the nature of dehiscence is not known. Pollen is apparently known only from permineralised material (Bose *et al.* 1985).

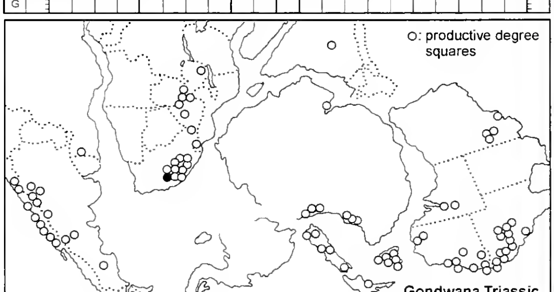
Specimens of *Sahnia* are rare in the fossil record:

- Drinnan & Chambers (1986); Koonwarra Lake deposit, Whitelaw road cutting, Victoria, mid-Cretaceous; three mature and six immature strobili recorded; several microsporangia illustrated.
- White (1981, 1986); Talbragar Fish Beds, latest Jurassic, New South Wales; two isolated strobili.
- Vishnu-Mittre (1953), Bose *et al.* (1985); Nipania, Rajmahal Hills, Bihar, India, Upper Jurassic to Lower Cretaceous; (?)two permineralised specimens, both multiple and attached.

GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION







Taeniopteris Brongn. 1832

Type species
Taeniopteris vittata Brongn. 1832?
Whitby, Yorkshire, England; Middle Jurassic.

Generic concept
A form-genus for simple strap-shaped leaves with entire lamina and lateral, parallel to occasionally forking venation at right angles to prominent midrib.

Generic characters
Leaf: small to large, simple strap-shaped, tapering at base; apex acute to obtuse; petiole short to absent, midrib prominent; venation at or close to right angles, parallel, forking once to occasionally twice, very rarely anastomosing.
Cuticle: see And. & And. (1989, p. 364); this vol., tf. 1 below.

Etymology
Taeniopteris—*taenia* (Lat.), ribbon; *pteris* (Lat.), fern.

Global range: numerous spp., Pangaea, U. C. to Recent.

Gondwana Triassic occurrence
Frequency (F): 32 degree squares (of the 84 across Gondwana).
Ubiquity (U): 5 continents (of 5 comprising Gondwana).
Diversity (D): 10 foliage species.
Abundance (A): 2% (the norm as in Molteno TCs).
Longevity (L): 20 myrs (Spathian to early Norian).

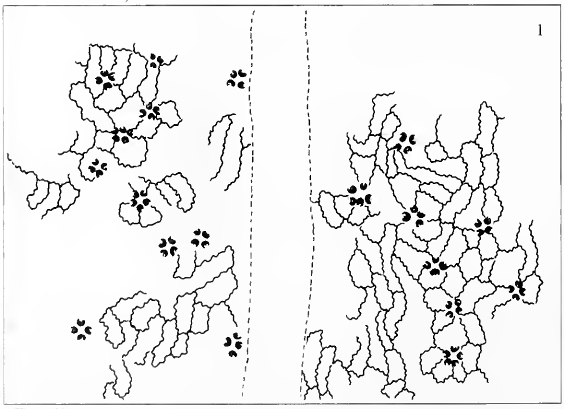
Colonisation success: FUDAL rating 32/5/10/2/20 = 69.
Intermediate success (Grade 3); *Taeniopteris* was the 4th most prominent genus in the Gondwana Triassic; it was frequent, diverse, ubiquitous, widespread and long-lived, but lacking in abundance.
Endemism: of the 10 described Gondwana Triassic species, 6 are more or less widespread, 3 are basin endemics, and 1 is a single-assemblage endemic.

Molteno occurrence
Frequency (F): 38 TCs (of 100 sampled in the Molteno).
Diversity (D): 8 species.
Abundance (A): abundant (10%) in 3 TCs; common (3–5%) in 3 TCs; occasional (1–2%) in 11 TCs; <1% in the other 21 TCs.

Habit: possibly woody shrubs to large trees, as suggested for *T. homerifolius* from the Molteno.
Preferred habitat: nearly ubiquitous in *Dicroidium* riparian forest (8 of 10 TCs), less frequent in open woodland (19 of 35 TCs) and lake-margin woodland (5 of 10 TCs).

Affiliated organs
Female strobilus: *Lindtheca*—Grade 3 with *T. homerifolius* (Kin. reinf., Mut. occ.).
Male strobilus: unknown.

from And. & And., 1989



1

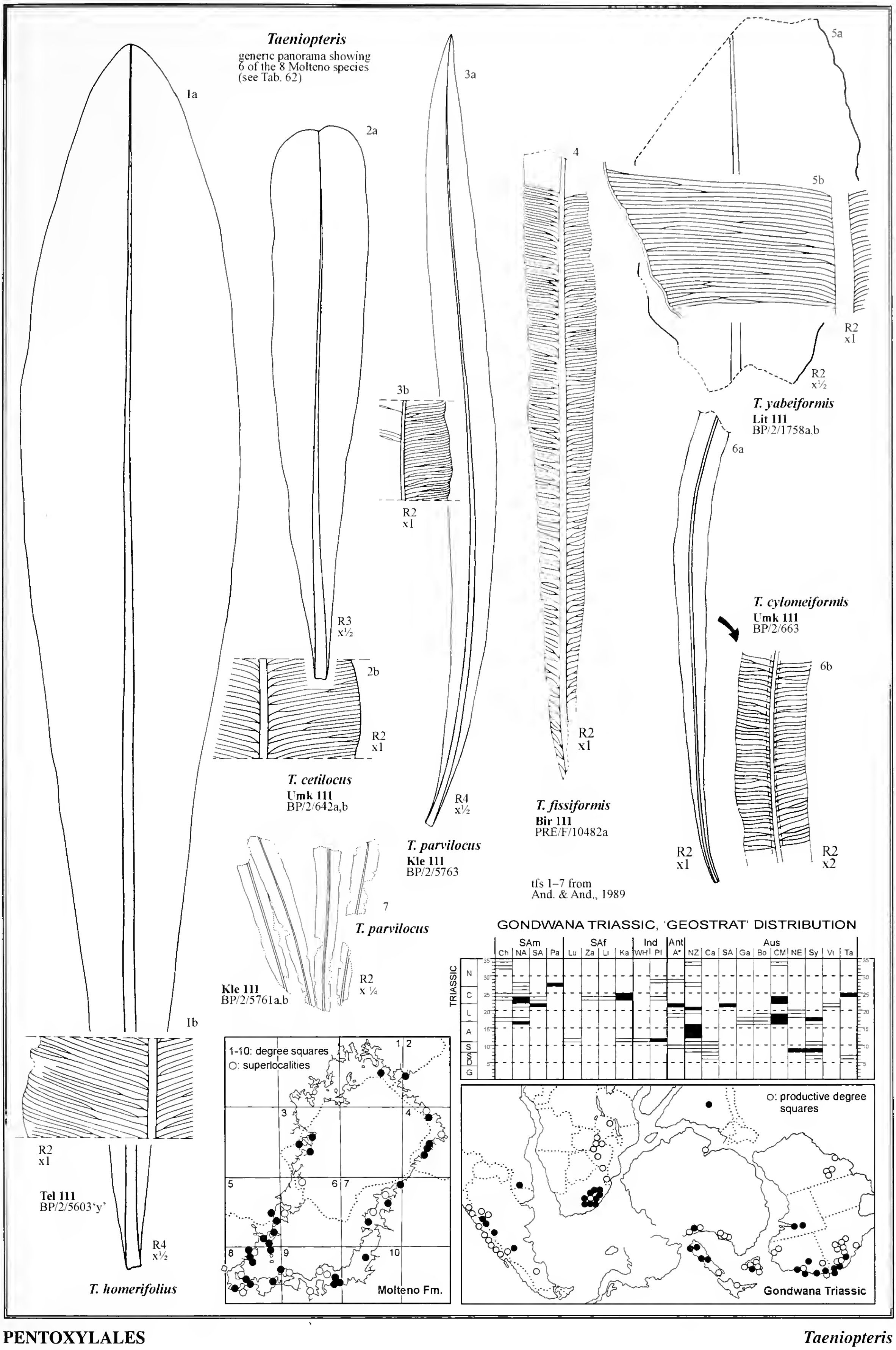
T. cetilocus **Lit 111** PRE/F/5518 x100

Classification & comparison
Suprageneric classification
While *Taeniopteris* is generally regarded as a form-genus, the affiliation (Grade 3) of the Molteno species, *T. homerifolius*, with *Lindtheca*, suggests that some forms of *Taeniopteris* may be placed in the Pentoxylales.
A similar case applies with regard to *Doratophyllum* Harris (1932). This *Taeniopteris*-like leaf has been found associated with the megasporophyll *Palaeocycas*. As these genera show cuticular correspondence, Florin (1933) erected the name *Bjuvia* for their combination.

Intergeneric comparison
Gondwana Triassic cycadopsid genera—The four cycadopsid genera (pp. 140–146) described from the Molteno all have divided laminae to some degree. They are quite distinct from *Taeniopteris*.
Other cycadopsid genera with similar leaf morphologies but not recorded from the Molteno are: *Nilssonia, Nilssoniopteris* and *Macrotaeniopteris* (see And. & And. 1989, p. 362). These all have characters that distinguish them from *Taeniopteris*.
Pentoxylalean genera—*Nipaniophyllum* Sahni (1948) is another *Taeniopteris*-like leaf. It has been found associated with cones and stems and has been placed in the order Pentoxylales (Sahni 1948; Stewart & Rothwell 1993).
Gnetopsid genera—Two Gondwana Triassic genera with taenioperoid venation, *Yabeiella* Oishi (1931), with a distinct marginal vein, and *Jungites*, were placed by us (And. & And. 1989) in the Gnetopsida on the basis of their very distinctive cuticle.

assemblages (taphocoenosis)		*Taeniopteris*	*T. cylomelformis*	*" fissiformis*	*" parvilocus*	*" anavolans*	*" cetilocus*	*" homerifolius*	*" yabeiformis*	*" sp.A (Kon 211*)*	*" spp. indet.*	*♀ Lindtheca*
Bir 111	Sph 2spp	70	-	10	-	5	-	55	-	-	-	-
Dor 111	Hei elo	**10**	-	-	**10**	-	-	-	-	-	-	-
Boe 111	Dic/Hei	**1**	-	-	1	4	-	**1**	-	-	-	-
Cyp 111	Dic cra	2	-	1	-	1	-	-	-	-	-	-
Kan 112	Hei elo	1	-	-	-	-	-	1	-	-	-	-
Tel 111	Hei elo	**2**	-	-	**1**	-	-	**1**	-	-	-	-
Vin 111	Dic odo	4	-	-	-	-	-	-	4	-	-	-
Ela 111	Dic odo	**1**	-	-	3	**1**	-	-	-	-	-	-
Kra 111	Dic odo	**5**	-	-	-	**4**	-	**1**	-	-	-	-
Lut 311	Hei elo	23	-	-	23	-	-	-	-	-	-	-
" 211	Sph pon	**10**	-	-	-	**10**	-	-	-	-	-	-
Tin 121	Sph 2spp	2	-	-	-	-	-	2	-	-	-	-
Wal 111	Dic odo	**3**	-	10	-	**3**	-	-	-	-	-	-
Kon 222	Dic odo	4	-	-	-	2	-	2	-	-	-	-
" 211	Ast 2spp	10	-	-	-	-	-	-	-	10	-	-
" 111	Dic odo	**1**	-	-	-	**1**	-	2	-	-	-	-
Pen 321	Dic/Ris	5	-	-	-	5	-	-	-	-	-	-
" 421	Dic odo	**2**	-	-	-	**2**	-	-	-	-	-	-
Kle 111	Hei/Dic	**5**	-	-	**5**	-	-	-	-	-	-	-
Kul 111	Sph pon	1	-	-	1	-	-	-	-	-	-	-
Kap 111	Dic/Ris	3	-	-	-	2	-	-	-	-	1	-
Nuw 111	Dic zub	1	-	-	1	-	-	-	-	-	-	-
Mor 111	Dic zub	**1**	-	-	**1**	-	-	-	-	-	-	-
" "	Dic odo	**2**	-	-	**2**	3	-	-	-	-	-	-
Mak 111	Dic odo	**10**	-	-	**10**	-	-	-	-	-	-	-
Maz 211	Hei/Dic	**1**	-	-	**1**	-	-	-	-	-	-	-
Hla 212	Dic 3spp	5	-	-	2	-	-	3	-	-	-	-
" 213	Dic elo	6	-	-	-	-	-	-	6	-	-	-
Umk 111	Dic 2spp	55	2	2	-	-	50	-	1	-	-	-
Inj 111	Dic odo	4	-	-	4	-	-	-	-	-	-	-
" 211	Dic dub	1	-	-	1	-	-	-	-	-	-	-
San 111	Dic cra	**2**	-	-	2	**2**	-	2	-	-	-	-
Mng 111	Dic 2spp	2	-	-	-	2	-	-	-	-	-	-
Mat 111	Dic dub	**2**	-	-	-	**2**	10	3	-	-	-	-
Gol 111	Dic dub	**1**	-	-	**1**	-	-	-	-	-	-	-
Lit 111	Dic/Hei	78	-	-	-	20	50	5	3	-	-	-
Aas 111	Hei elo	2	-	-	-	2	-	-	-	-	-	-
" 411	Dic/Sph	**1**	-	-	-	-	-	**1**	-	-	-	16
Total TCs		38	1	4	17	18	3	13	4	1	1	1

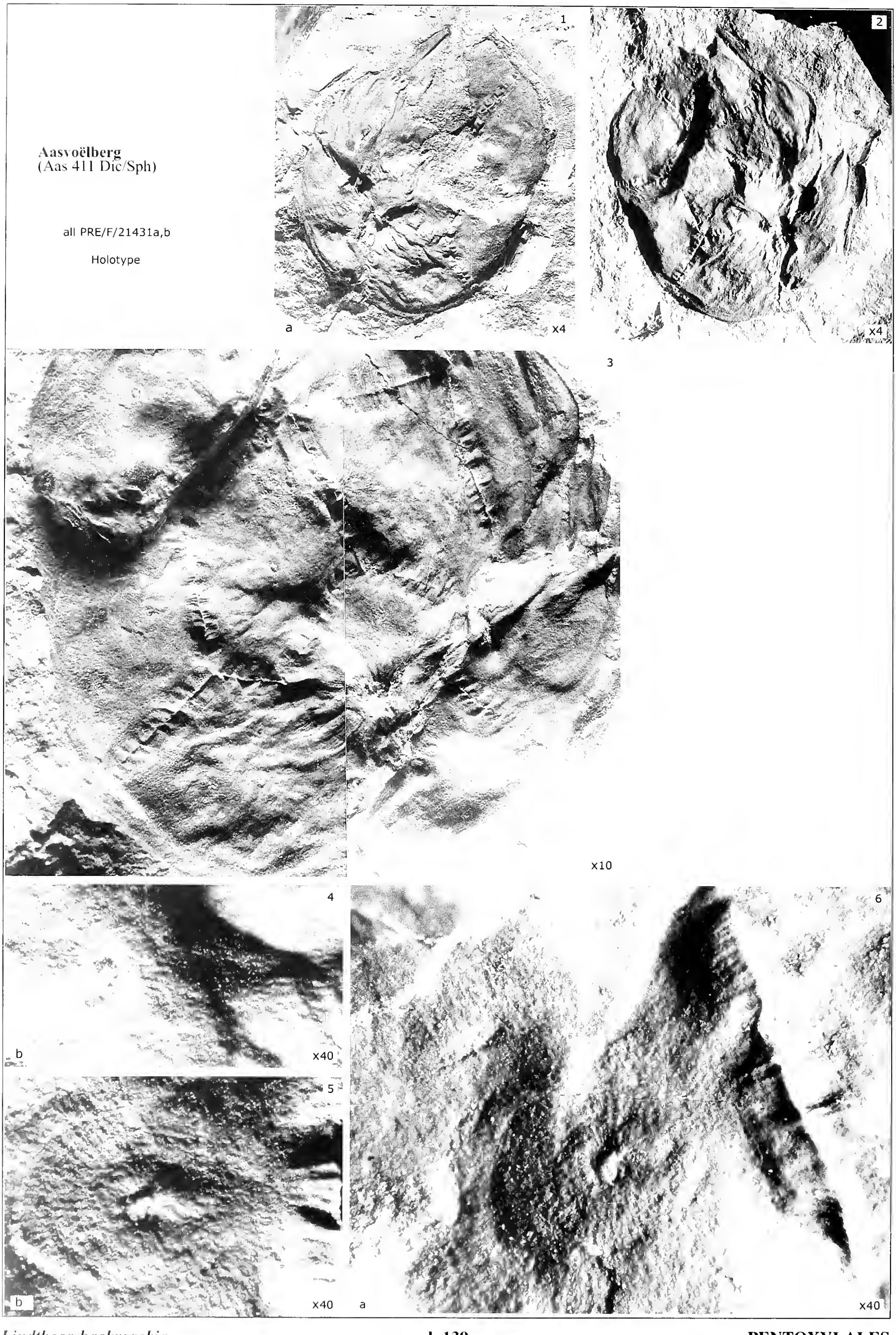
Tab. 62. ***Taeniopteris*, Molteno occurrence**

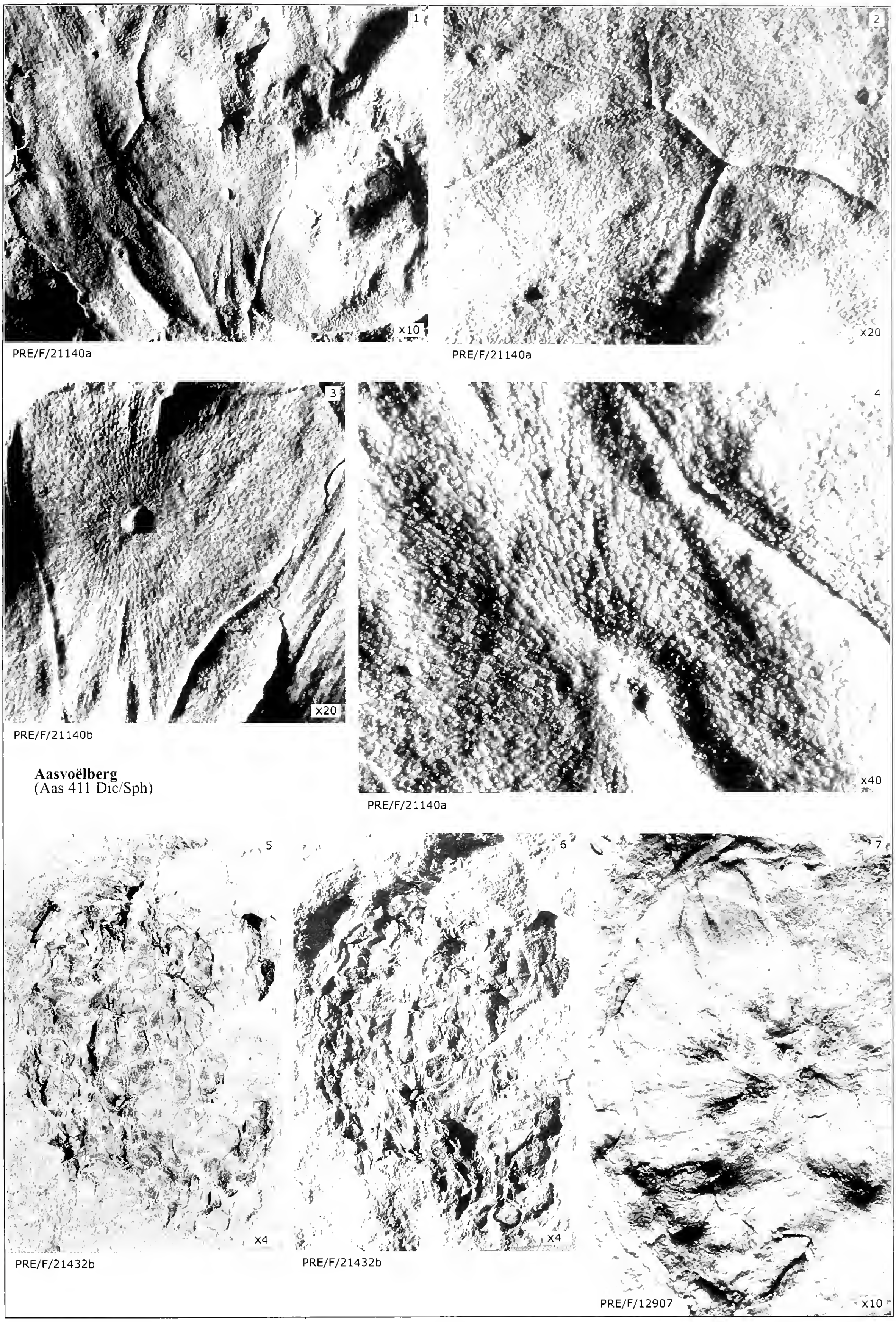

Taeniopteris
generic panorama showing 6 of the 8 Molteno species (see Tab. 62)
1a
1b
R2 x1
Tel 111
BP/2/5603'y'
R4 x½
T. homerifolius
2a
R3 x½
2b
R2 x1
T. cetilocus
Umk 111
BP/2/642a,b
3a
3b
R2 x1
R4 x½
T. parvilocus
Kle 111
BP/2/5763
4
R2 x1
T. fissiformis
Bir 111
PRE/F/10482a
5a
5b
R2 x1
R2 x½
T. yabeiformis
Lit 111
BP/2/1758a,b
6a
R2 x1
T. cylomeiformis
Umk 111
BP/2/663
6b
R2 x2
7
T. parvilocus
Kle 111
BP/2/5761a,b
R2 x ¼
tfs 1–7 from And. & And., 1989
GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION
SAm SAf Ind Ant Aus
Ch NA SA Pa Lu Za Li Ka WH Pl A* NZ Ca SA Ga Bo CM NE Sy Vi Ta
TRIASSIC
N C L A S S D G
35 30 25 20 15 10 5
1-10: degree squares
○: superlocalities
Molteno Fm.
○: productive degree squares
Gondwana Triassic

Aasvoëlberg
(Aas 411 Dic/Sph)

all PRE/F/21431a,b

Holotype




1
x10
PRE/F/21140a
2
x20
PRE/F/21140a
3
x20
PRE/F/21140b
4
x40
PRE/F/21140a
Aasvoëlberg
(Aas 411 Dic/Sph)
5
x4
PRE/F/21432b
6
x4
PRE/F/21432b
7
x10
PRE/F/12907

GNETOPSIDA Pilg. & Melch. 1954
NATALIGMALES J.M.And. & H.M.And., ord. nov.
NATALIGMACEAE J.M.And. & H.M.And., fam. nov.

Nataligma J.M.And. & H.M.And., gen. nov.

Type species
Nataligma dutoitii J.M.And. & H.M.And., sp. nov.
Umkomaas Valley, Karoo Basin, S. Africa, Carnian, Triassic.

Generic diagnosis
A stem-gnetopsid ovulate compound strobilus comprising a series of whorls of small whorled ovate strobili (cones) borne on elongated slender axes.

Generic characters
Compound strobilus: primary axis linear, gracile (*ca* 2 mm diam.), smooth; strobili in widely spaced whorls (up to 50 mm apart) of *ca* 8 units along axis.
Strobilus: ovoid, compact, cone-like, small (*ca* 5 x 8 mm); axis gracile, long (*ca* 15–20 mm), curving upwards; megasporophylls numerous, in *ca* 6 whorls (of up to 10 units) per cone.
Megasporophyll: apparently a simple scale; distal laminae rounded, imperfectly demarcated and forming a continuous shell; possible trichomes visible as 2 or 3 linear parallel to spreading marks per lamina, and more evidently extending from distal end of cone; peduncle gracile.
Ovule: unknown.

Etymology
Nataligma—an intriguing enigma from the province of Natal.

Global range: 1 sp., Gondwana, Tr. (CRN).
First & last: Molteno Fm.

Gondwana Triassic occurrence
SAf—Karoo Basin, one TC (5 indivs).

Molteno occurrence
Frequency (F): 1 TC (of 100 sampled in the Molteno).
Diversity (D): 1 species.
Abundance (A): 4 indivs; extremely rare.
Umk 111 Dic 2spp: 4 indivs in 400 man-hours (1 per 8 man-days), extremely rare

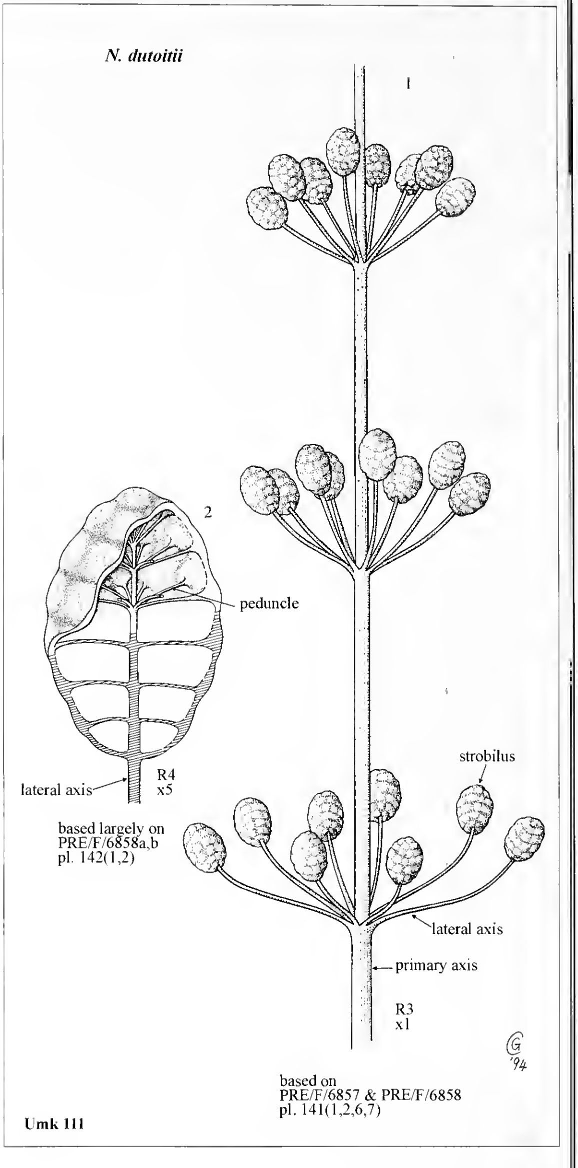
Affiliated organs
Male strobilus: unknown.
Foliage: *Gontriglossa*—Grade 2 (Mut. occ., Mor. cor.).

Classification & comparison
Suprageneric classification (Nataligmaceae/Nataligmales)
We originally placed this compound strobilus in the Sphenophyta (And. & And. 1983, pl. 21, fig. 1) based on the whorls of cones along the axis. However, the Molteno axis lacks the striations generally characterising sphenophyte stems. The individual cones of *Nataligma* do somewhat resemble *Echinostachys* cones which have been found attached to *Schizoneura* stems with leaves coming from the same whorl. However, the cones of *Echinostachys* show distinct scales in outer view. Their detailed structure is now known (Grauvogel-Stamm 1978; Grauvogel-Stamm & Ash 1999).

Amongst the gymnosperms, the only groups of which we are aware that bear whorled fruiting structures are the Gnetopsida (extant) and the Fredlindiales (Gondwana Triassic). Is there a shared plesiomorphic character involved, or is the similarity an expression of convergent evolution? The small individual cones of *Nataligma* are certainly unlike anything within these two groups.

Nataligma is included here, alongside the Fraxinopsiales, primarily on the basis of the cuticular similarities between their foliage affiliates (Grade 4 reliability in the latter, but only Grade 2 in the former). The pair are placed in the class Gnetopsida in view of their shared, possibly symplesiomorphic, whorled character. *Fraxinopsis* in turn has a possible link to *Dechellyia*, Late Triassic, USA (see box, p. 373), which has been classified in the Gnetopsida (Ash 1972; Crane 1988). *Nataligma* is placed in the new order Nataligmales and new family Nataligmaceae within the class Gnetopsida.

Intergeneric comparison (Gondwana Triassic): nothing similar.



Reconstructions
The holotype, pl. 141(1–4), shows two whorls of strobili. The primary axis is of similar width for 88 mm, an indication that the total length was probably far greater. A second specimen, with one whorl, pl. 141(5–8), could be a part of the holotype as it matches in size—but the cleavage does not fit owing to missing rock matrix. We have drawn the compound strobilus with three whorls, leaving the proximal and distal ends incomplete.

The nature of the individual strobilus or cone is evident in PRE/F/6858a,b, pl. 142(1–3), where six whorls are visible. These whorls of pedicellate scales (megasporophylls) blend into the glossy carbonaceous matrix. Two or three fine linear striations which may represent trichomes are seen repeated on each of the ill-defined distal laminae [PRE/F/6857a,b, pl. 142(4–6)]. On another isolated strobilus, PRE/F/6859b, a pair of possible trichomes can be seen to arise from the apex of the cone, pl. 142(7, 8), as does a single hair from the left side of the strobilus, pl. 142(9).

Evidence for affiliation of organs

Mutual occurrence

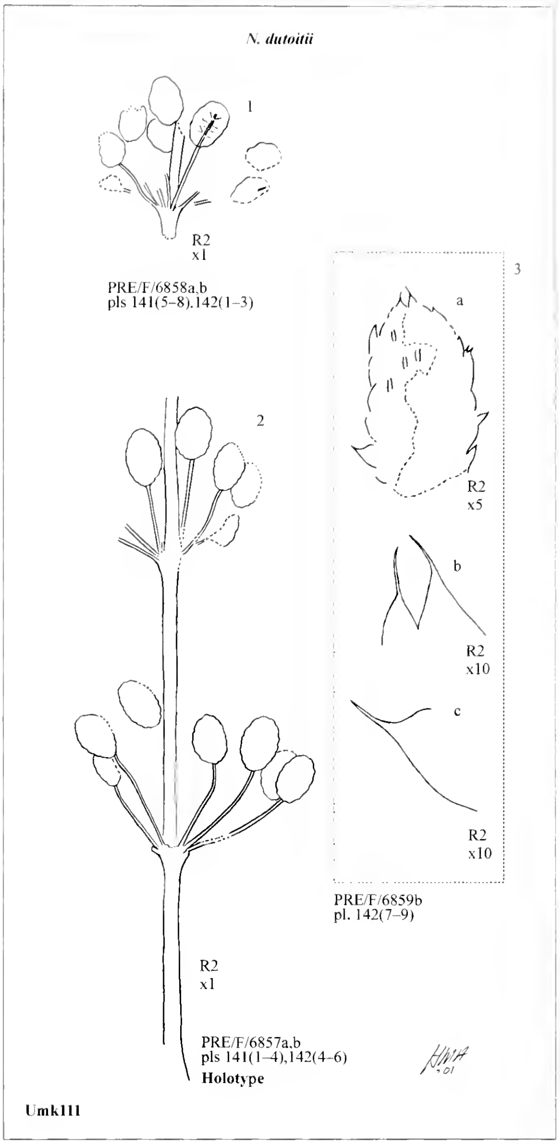
Nataligma is found only at Umk 111, which also yields *Gontriglossa verticillata* (Tabs 25, 26).

Morphological correspondence

The primary axis (stem) of this compound strobilus is very similar to the stem of *Gontriglossa verticillata* (And. & And. 1989), which bears leaves in apparent whorls (composed of opposite fascicles) at regularly spaced nodes (*ca* 100 mm apart). A good collection of *G. verticillata*, including three stems with leaves attached, is known from the same TC (Umk 111) as *Nataligma*. On the basis of similar morphology—a stem with leaves or cones in whorls—we place *Nataligma* as an affiliate (Grade 2) of *Gontriglossa verticillata*.

Cuticles

Potential sample: Umk 111, 4 indivs.
Macerated (this work): 2 indivs (8 samples).
Preservation grade: Grade 1.
Diagnostic characters: —
Comment: Microscopic details remain unknown for this Molteno cone, the eight carbonaceous samples macerated having yielded no definable morphology. The cuticle is apparently quite altered.
Significance: of no aid in classification or affiliation.



Nataligma dutoitii J.M.And. & H.M.And., sp. nov.

Holotype

Specimen: PRE/F/6857a,b; pls 141(1–4), 142(4–6).
Assemblage (TC): Umk 111 Dic 2spp, Umkomaas Valley.
Preservation: middle section of strobilus, part and counterpart; compression in thinly laminated, carbonaceous (good cuticle), moderately baked, dark grey shale with good cleavage.

Reference palaeodeme

Assemblage (TC): as for holotype.
Specimens: 4 indivs (2 intact strobili, 2 isolated cones), pls 141, 142.

Specific diagnosis—as for genus.

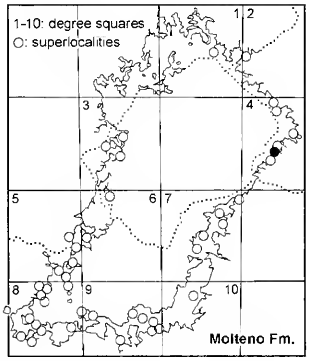
Specific characters—as for genus.

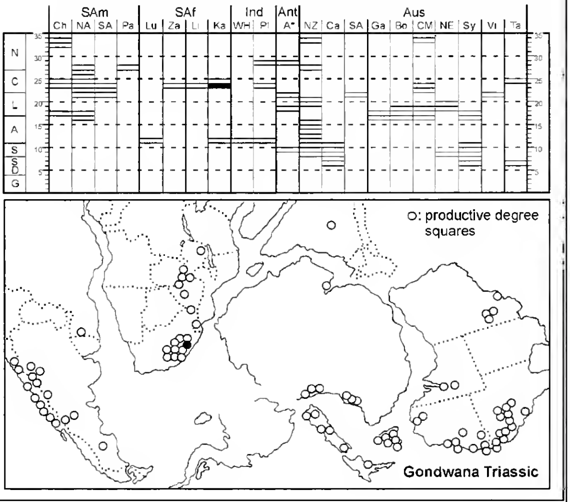
Eponymy

dutoitii—in honour of Alexander du Toit, the greatest of South African geologists and a pioneer in the study of the Molteno palaeoflora.

Comment & comparison—as for genus.

GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION





Gontriglossa J.M.And. & H.M.And. 1989

Type species

Gontriglossa verticillata (Thomas 1958) J.M.And. & H.M.And. 1989. Umkomaas Valley, Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis

A stem-gnetopsid vegetative genus comprising long shoots bearing opposite fascicles of narrowly elliptic leaves, with frequently anastomosing open-mesh arching venation, at regularly spaced nodes.

Generic characters

Foliage shoot: leaves apparently attached in whorls comprising opposite fascicles of 3 leaves at regularly spaced nodes (*ca* 100 mm apart); shoot slender (4–6 mm diam.), with indistinct longitudinal striations.

Leaf: medium (110 x 25 mm); petiole stout, moderately long; lamina narrowly elliptic, margin entire to irregularly wavy, apex obtuse; midrib distinct, veins at steep angle (*ca* 50°) from horizontal, arching strongly to margin, frequently anastomosing, mesh open, length to width ratio 10:1 near midrib and decreasing strongly to margin.

Cuticle: see And. & And. (1989, p. 505); this vol., tf. 4 opposite.

Etymology

Gontriglossa—a combination word referring to *Glossopteris*-like leaves from the Gondwana Triassic.

Global range: 1 sp., Gondwana, U. Tr. (LAD–CRN).

First: *Glossopteris* (*Gontriglossa*) *grandis* (Holmes 1992); Basin Creek Fm., Nymboida, N.S.W., Australia.

Last: the Molteno species.

Gondwana Triassic occurrence

Frequency (F): 10 degree squares (of the 84 across Gondwana).

Ubiquity (U): 4 continents (of 5 comprising Gondwana).

Diversity (D): 1 foliage species.

Abundance (A): 1% (the norm as in Molteno TCs).

Longevity (L): 9 myrs (Ladian to Carnian).

Colonisation success: FUDAL rating 10/4/1/1/9 = 25.

Limited success (Grade 2); *Gontriglossa* was the 13th most prominent genus in the Gondwana Triassic; it was moderately frequent, ubiquitous, long-lived and common, but markedly lacking in diversity.

Endemism: The single species, *G. verticillata*, had a wide distribution, being known from four Gondwana continents.

Molteno occurrence

Frequency (F): 8 TCs (of 100 sampled in the Molteno).

Diversity (D): 1 species.

Abundance (A): common (5%) in 1 TC; occasional (1–2%) in 2 TCs; rare to extremely rare (<1%) in 5 TCs.

Habit: possibly a slender herbaceous pioneer.

Preferred habitat: frequent in the *Dicroidium* riparian forest (6 of 10 TCs); also found in fern/horsetail meadows (wetlands).

Affiliated organs

Female strobilus: *Nataligma*—Grade 2 (Mut. occ., Mor. cor.).

Male strobilus: unknown.

Classification & comparison

Intergeneric comparison

Three historical genera in particular, all erected in the 19th century, have been repeatedly employed in the Gondwana Triassic literature for *Gontriglossa verticillata* leaves: *Glossopteris*, *Sagenopteris* and *Anthrophyopsis* (And. & And. 1989, pp. 504, 505).

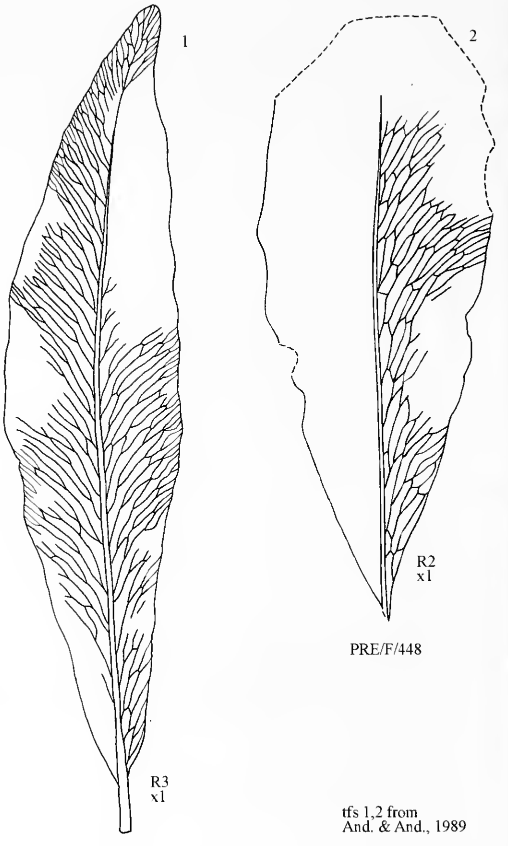
Glossopteris Brongn. 1828 (dominant in the Gondwana Permian)—is superficially indistinguishable from *Gontriglossa*, but the cuticle and mode of attachment are different.

Sagenopteris Presl 1838 (the foliage of the *Caytonia* plant)—was widespread in Laurasia and ranged from the Upper Triassic to the Upper Cretaceous (Crane 1985). *G. verticillata* may be confused with the individual leaflets of *Sagenopteris*, but the latter is a compound, superficially palmate leaf, with two pairs of readily dehiscing, sessile leaflets, attached apically on a long petiole, and it has a cuticle with anomocytic stomata and cells of a regular shape with straight to sinuous walls (Harris 1964; Crane 1985).

Anthrophyopsis Nathorst 1878 (Rhaetic of Sweden and Greenland)—has cuticle which is also quite different from *G. verticillata*. Its mode of attachment and reproductive organs are unknown.

G. verticillata

the single species from the Molteno



PRE/F/442

PRE/F/448

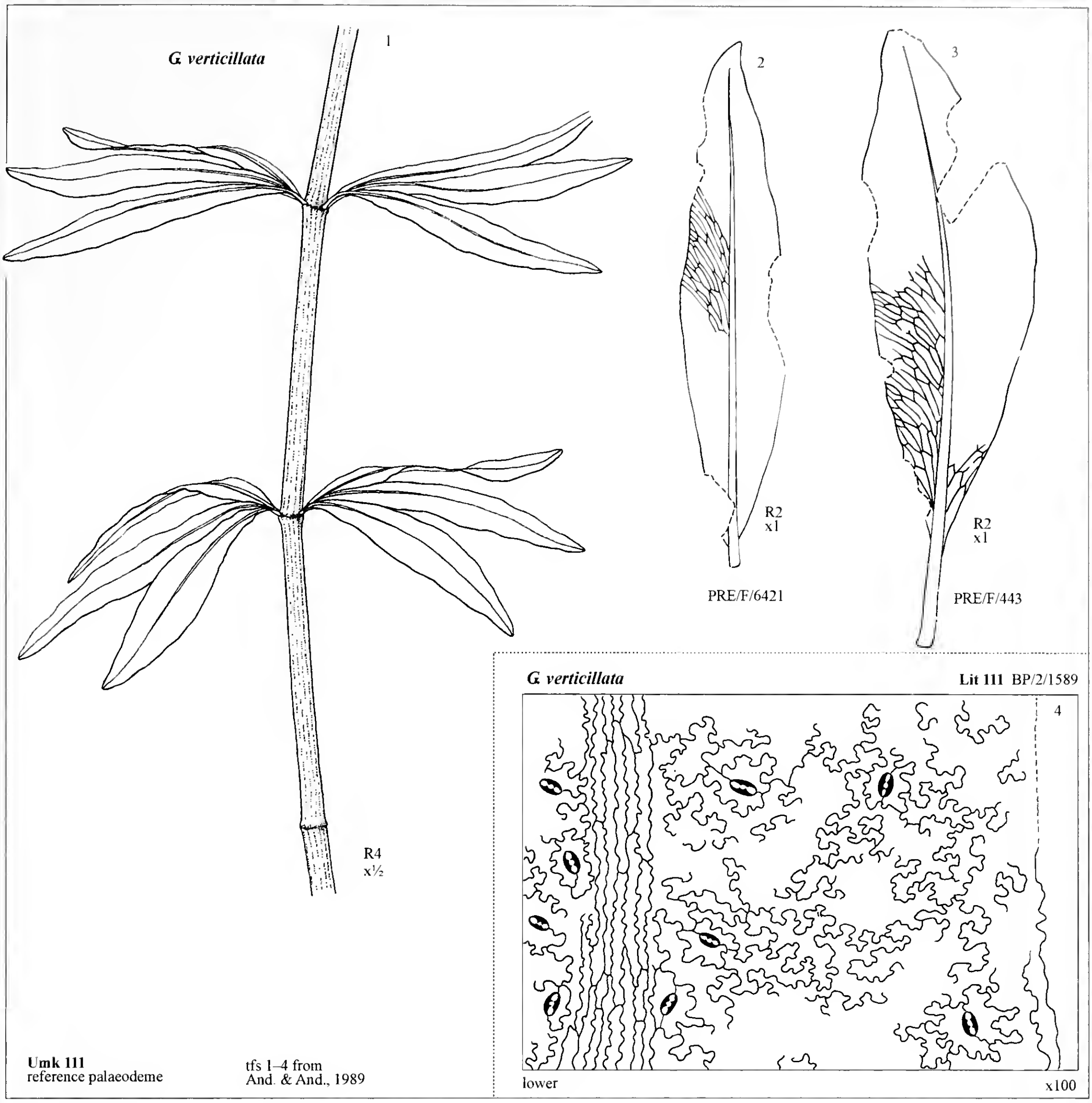
tfs 1,2 from And. & And., 1989

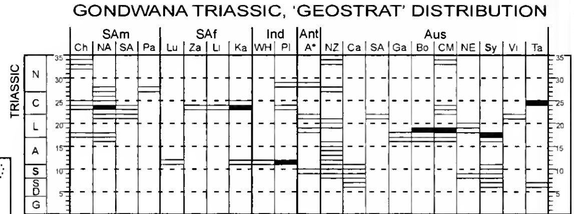
Umk 111

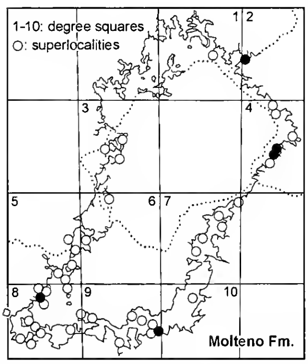
reference palaeodeme

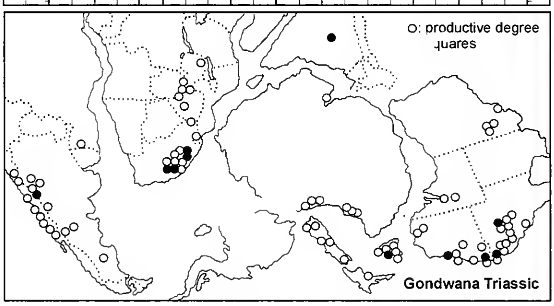
Among Gondwana Triassic foliage genera, *G. verticillata* has much in common with *Yabeiella* (widespread and common) and *Jungites* (exclusive to the Molteno). Each shows anastomosing venation to lesser or greater extent and their cuticles are similar in having amorphously shaped non-papillate cells with strongly meandering walls. While the cuticles of *Yabeiella* and *Jungites* are very close, that of *G. verticillata* differs in having paracytic stomata and complex digitately amorphous cell outlines. It seems likely that the three genera, together with *Graciliglossa* and *Cetiglossa*, comprise a natural group or clade, here included in the Gnetopsida.

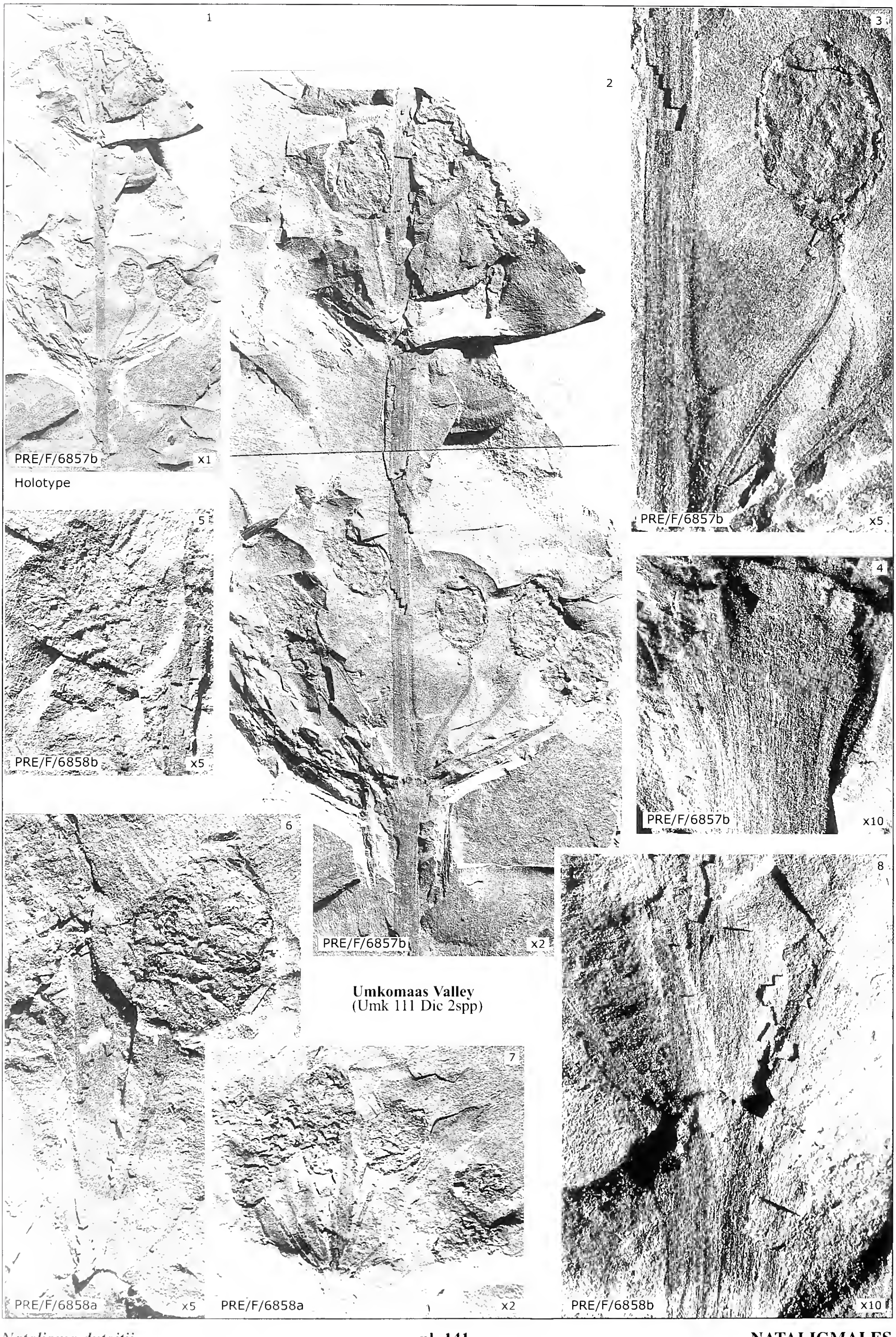
Holmes (1992) placed certain Australian Triassic leaves in the genus *Glossopteris*—while emphasising that *Glossopteris* was used as a form genus and that no relationship with Permian *Glossopteris* was inferred. *Glossopteris grandis* (Walkom) Holmes has whorls of up to 10 leaves which appear, individually, to be closely similar to *Gontriglossa verticillata*. However, the form of attachment to a stem is not clear, so close relationship cannot be made with the Molteno material.


G. verticillata
1
2
3
R2
x1
R2
x1
PRE/F/6421
PRE/F/443
R4
x½
G. verticillata
Lit 111 BP/2/1589
4
Umk 111
reference palaeodeme
tfs 1–4 from
And. & And., 1989
lower
x100

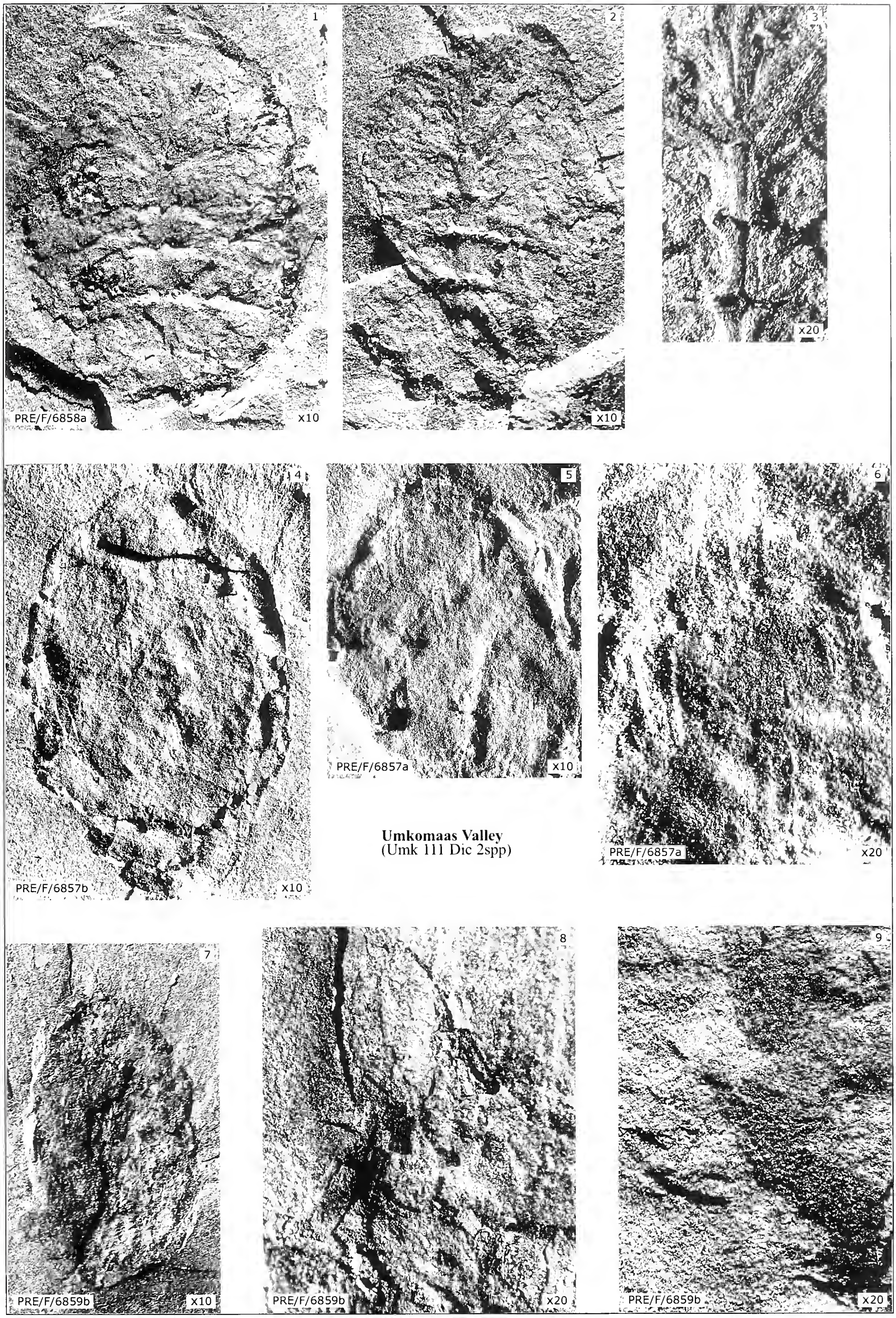

GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION
SAm
SAf
Ind
Ant
Aus
Ch NA SA Pa Lu Za Li Ka WH Pl A* NZ Ca SA Ga Bo CM NE Sy Vi Ta
TRIASSIC
N
C
L
A
S
S
D
G


1-10: degree squares
O: superlocalities
1 2
3
4
5
6 7
8
9
10
Molteno Fm.


O: productive degree squares
Gondwana Triassic



Umkomaas Valley
(Umk 111 Dic 2spp)


1
PRE/F/6858a
x10
2
x10
3
x20
4
PRE/F/6857b
x10
5
PRE/F/6857a
x10
6
PRE/F/6857a
x20
Umkomaas Valley
(Umk 111 Dic 2spp)
7
PRE/F/6859b
x10
8
PRE/F/6859b
x20
9
PRE/F/6859b
x20

GNETOPSIDA Pilg. & Melch. 1954
INCERTAE SEDIS order
INCERTAE SEDIS family

Graciliglossa J.M.And. & H.M.And., gen. nov.

Type species
Gontriglossa hilaryjanea J.M.And. & H.M.And. 1989.
Umkomaas Valley, Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis
A stem-gnetopsid leaf of small gracile form, oblong-lanceolate shape with cordate base and entire margin, and frequently anastomosing venation with open mesh at steep angle to margin.

Generic characters
Leaf: small (60 x 15 mm), gracile, oblong-lanceolate, base cordate-sagittate, apex obtuse, lamina margin entire; petiole gracile, seemingly short; midrib distinct; veins at very steep angle (*ca* 70–80°) from horizontal, not arching to margin, frequently anastomosing, mesh open, length to width ration 6:1 near midrib and decreasing strongly to margin, with distinctive marginal vein parallel to cordate base.
Cuticle: unknown.

Etymology
Graciliglossa—*gracilis* (Lat.), gracile, thin, slender; *glossa* (Gr.), tongue; referring to the gracile, tongue-shaped leaf.

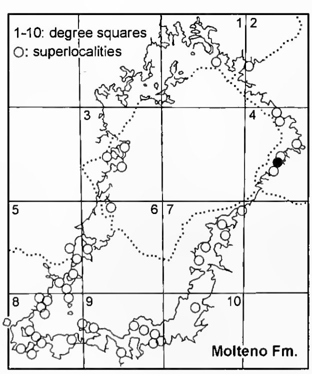
Global range: 1 sp., Gondwana, U. Tr. (CRN).
First & last: the Molteno species described here.

Gondwana Triassic occurrence
Frequency (F): 1 degree square (of the 84 across Gondwana).
Ubiquity (U): 1 continent (of 5 comprising Gondwana).
Diversity (D): 1 foliage species.
Abundance (A): <1% (as recorded in the Molteno).
Longevity (L): 1 myr (Lower Carnian).
Colonisation success: FUDAL rating 1/1/1/–/1= 4.
Minimum success (Grade 1); *Graciliglossa* was an extremely minor component of the Molteno flora.
Endemism: the single species, *G. hilaryjanea*, as known, is a single-assemblage endemic.

Molteno occurrence
Frequency (F): 1 TC (of 100 sampled in the Molteno).
Diversity (D): 1 species.
Abundance (A): very rare (<1%) in the 1 TC.
Habit: possibly a slender, herbaceous pioneer.
Preferred habitat: *Dicroidium* riparian forest.

Affiliated organs: unknown.

Classification & comparison
We have transferred this leaf to a new genus distinct from *Gontriglossa* because of its small size, gracile axis and petiole, cordate base with marginal vein and the lack of specimens showing the attachment of leaves as found in that taxon (see further under *Cetiglossa*, p. 369).
No similar leaf is known from the Gondwana Triassic, but in the Permian certain *Glossopteris* leaves have a cordate base and open anastomosing veins.



Graciliglossa hilaryjanea J.M.And. & H.M.And., comb. nov.

Holotype
Specimen: BP/2/590; And. & And. [1989, pl. 309(3, 14)].
Assemblage (TC): Umk 111 Dic 2spp, Umkomaas Valley.
Preservation: nearly complete leaf, without counterpart; compression in thinly laminated, carbonaceous (good cuticle), moderately baked, dark grey shale with good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 13 indivs [And. & And. 1989, pls 309(1–22), 310(1–11)].

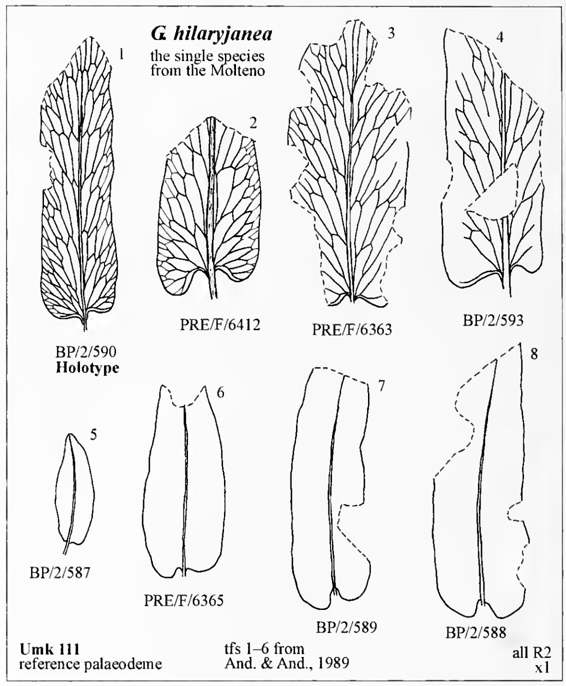
Sister palaeodemes—none.

Specific diagnosis—as for genus.

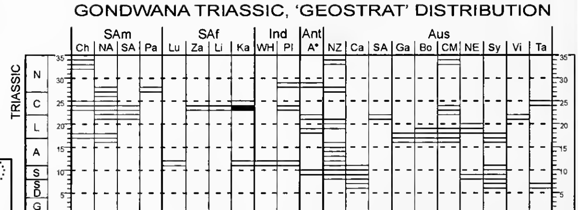
Specific characters—as for genus.

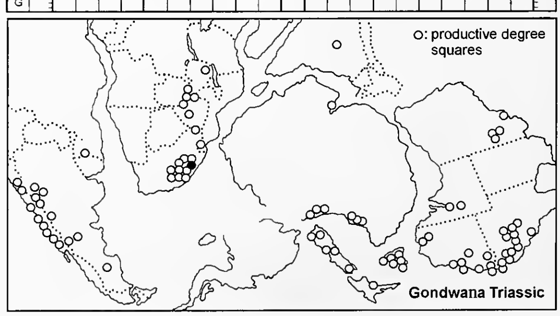
Eponymy
hilaryjanea—for our daughter Hilary Jane, who is a gracile child and who has accompanied us on several collecting trips.

Comment & comparison
No similar leaf is known from the Gondwana Triassic.



GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION





GNETOPSIDA Pilg. & Melch. 1954
INCERTAE SEDIS order
INCERTAE SEDIS family

Cetiglossa J.M.And. & H.M.And., gen nov.

Type species
Gontriglossa balaena J.M.And. & H.M.And. 1989.
Umkomaas Valley, Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis
A stem-gnetopsid leaf of large size, broadly elliptic shape with irregularly crenulate margin, and frequently anastomosing venation with elongate parallel mesh at moderate angle to margin.

Generic characters
Leaf: large (up to >110 mm long), broadly elliptic, apex probably obtuse; lamina margin irregularly crenulate; petiole unknown; midrib distinct, veins at moderate angle (*ca* 40–45°) from horizontal, very faintly sinuous to margin, frequently anastomosing, mesh elongate, length to width ratio *ca* 15:1 near midrib and decreasing strongly to margin.
Cuticle: unknown.

Etymology
Cetiglossa—*cetis* (Lat.), whale; *glossa* (Gr.), tongue; with reference to the tongue-shaped leaf from the Umkomaas locality.

Global range: 1 sp., Gondwana, U. Tr. (CRN).
First & last: the Molteno species described here.

Gondwana Triassic occurrence
Frequency (F): 1 degree square (of the 84 across Gondwana).
Ubiquity (U): 1 continent (of 5 comprising Gondwana).
Diversity (D): 1 foliage species.
Abundance (A): <1% (as recorded in the Molteno).
Longevity (L): 1 myr (Lower Carnian).

Colonisation success: FUDAL rating 1/1/1/–/1=4.
Minimum success (Grade 1); *Cetiglossa* was an extremely minor component of the Molteno flora.
Endemism: the single species, *C. balaena*, as known, is a single-assemblage endemic.

Molteno occurrence
Frequency (F): 1 TC (of 100 sampled in the Molteno).
Diversity (D): 1 species.
Abundance (A): extremely rare (<1%) in the single TC.

Habit: possibly a slender herbaceous pioneer.
Preferred habitat: *Dicroidium* riparian forest.

Affiliated organs: unknown.

Comparison & classification
Intergeneric comparison
In And & And. (1989), the three species, *Cetiglossa balaena, Graciliglossa hilaryjanea* and *Gontriglossa verticillata*, were all included in the genus *Gontriglossa*. These are now placed in three distinct genera, reflecting a more natural classification, we believe. The changes are based on the following reasoning:

1) Although all three species have clear midribs and reticulate venation, they differ particularly widely in size, leaf shape and nature of the anastomosing veins.
2) *Gontriglossa verticillata* has yielded very characteristic Grade 3 cuticle, while *Graciliglossa hilaryjanea* and *C. balaena* have yielded only Grade 1 cuticle without interpretable structures. Were the three species of the same genus, one might expect all to yield cuticle of similar quality.
3) While *Gontriglossa verticillata* has been found frequently with leaves attached to a stem, the other taxa are unknown in this state. This suggests modes of attachment that might have been significantly different.

Subject to confirmation, based on a good deal more information than the foliage alone, we place *Cetiglossa* and *Graciliglossa* in separate families but a single order (all unnamed), probably distinct from the Natatigmales (see pp. 21, 55).

Santaecruzia (Gnaedinger & Herbst 1998) was based on Gondwana material from the Upper Triassic of Argentina. The genus has much finer, closer-spaced anastomosing venation than *Cetiglossa* and the veins emerge at an angle of 90° to the midrib.

Cetiglossa balaena (J.M.And. & H.M.And. 1989) J.M.And. & H.M.And., comb. nov.

Holotype
Specimen: PRE/F/750; And. & And. [1989, pl. 308(4, 6–9)].
Assemblage (TC): Umk 111 Dic 2spp, Umkomaas Valley.
Preservation: incomplete leaf, without counterpart; compression in thinly laminated, carbonaceous (good cuticle), moderately baked, dark grey shale with good cleavage.

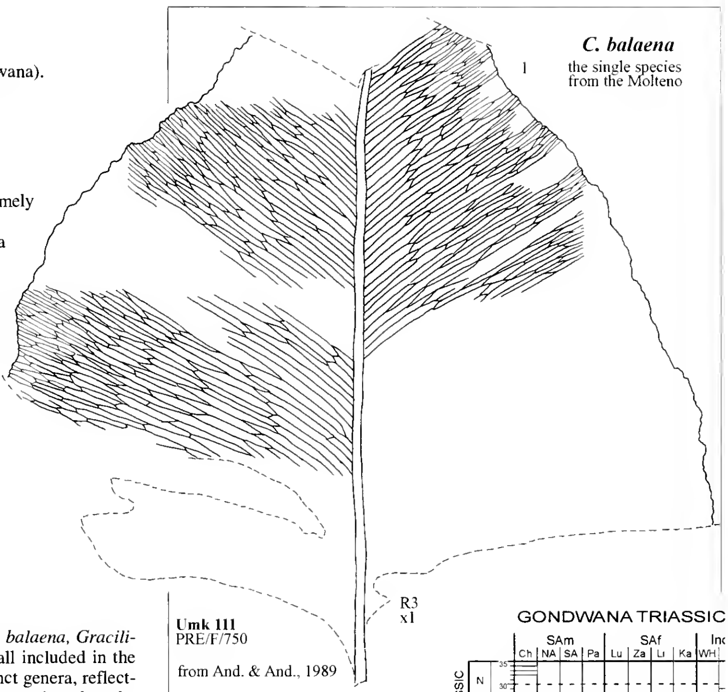
Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 3 indivs (And. & And. 1989, pl. 308).

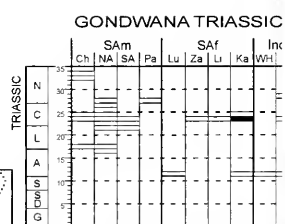
Species diagnosis—as for genus.

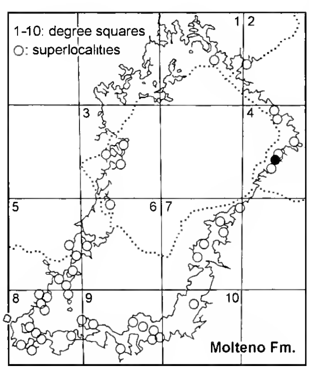
Species description—as for genus.

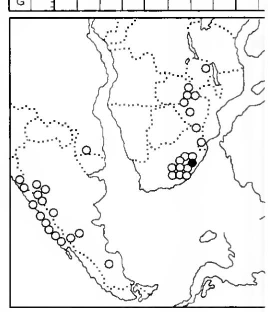
Etymology
balaenus (Lat.)—whale, after the type locality Umkomaas (meaning cow or whale in the local Zulu language).

Comment & comparison
Glossopteris nymboidensis Holmes (1992), from the Middle Triassic Basin Creek Fm., Nymboida Coal Measures, Australia, is close to *C. balaena*, but differs in the still narrower, more elongate venation mesh and in the decurrent lateral veins which leave the midrib at an acute angle, then arch and continue straight and parallel towards the margin at *ca* 75°.









GNETOPSIDA Pilg. & Melch. 1954
FRAXINOPSIALES J.M.And. & H.M.And., ord. nov.
FRAXINOPSIACEAE J.M.And. & H.M.And., fam. nov.

Fraxinopsis Wieland 1929

Type species
Fraxinopsis minor Wieland 1929.
Minas de Petroleo, Cacheuta Basin, South America. Potrerillos Fm., L. Carnian, Triassic.

Generic concept
A stem-gnetopsid dispersed seed (strobilus unknown), comprising a small seed body with longitudinal groove, and a large, elongate leaf-like wing with parallel veins that may bifurcate and anastomose.

Generic characters
Strobilus: unknown.
Megasporophyll: unknown.
Seed: winged, small to large (*ca* 12–>50 mm long); seed body relatively small, elliptical, with a distinct longitudinal groove, glabrous to densely hairy, with incipient to pronounced distal auricular lobes; wing leaf-like, relatively large, elongate to oval-elliptic, 2–5 times the length of the seed body, glabrous to hirsute; veins clearly developed, *ca* 6–16 at widest point, parallel and rarely to commonly bifurcating and anastomosing.

Etymology
Fraxinopsis—after the extant genus *Fraxinus*, whose seeds Wieland (1929) considered similar to his fossil material.

Global range: several spp., Gondwana, Tr. (CRN).
First: *Fraxinopsis major* (Jones & De Jersey 1947); Tivoli Stage, Ipswich CM, Queensland, Australia.
Last: *Fraxinopsis andium*; Molteno Fm.

Gondwana Triassic occurrence
SAm—N. Argentina; Cacheuta Basin, 4 locs (many indivs reported); Barreal-Hilario Basin; 2 locs (6 indivs illustr.).
SAf—Karoo Basin (Molteno Fm.); 17 TCs (292 curated indivs).
Aus—Queensland; Ipswich Coalfield, 11 locs (many indivs reported).

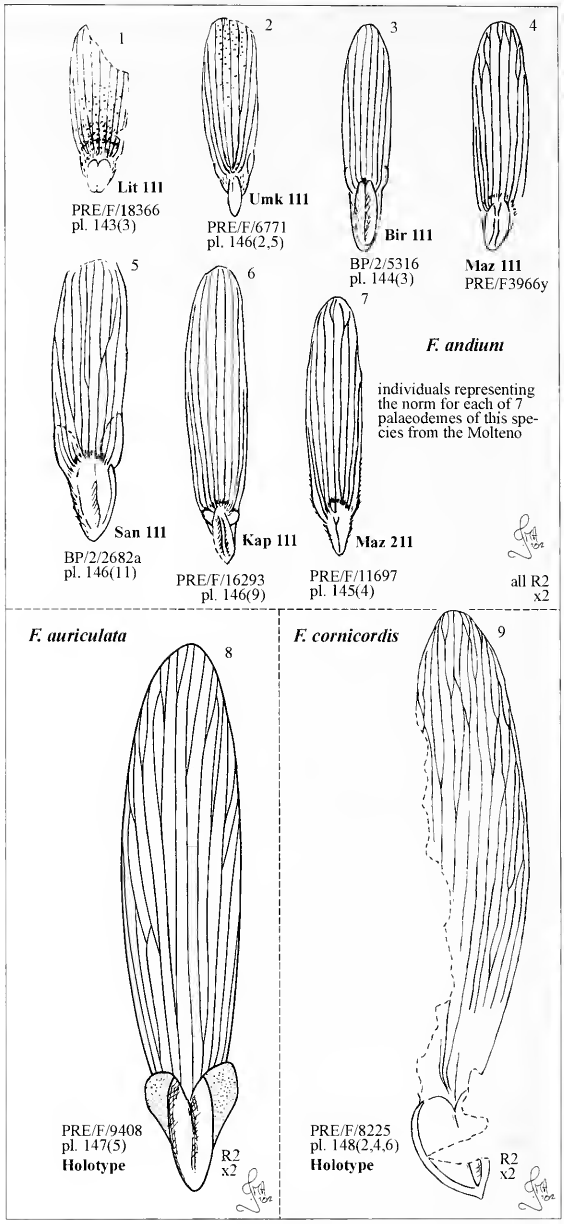
Molteno occurrence
Frequency (F): 18 TCs (of 100 sampled in the Molteno).
Diversity (D): 3 species.
Abundance (A): 306 indivs total; rare to extremely rare in top 9 TCs.

Kra 311 Dic odo:	>35	indivs	in	13	man-hrs	cleaving	(>10	per	1	man-day)	rare
Maz 211 Hei/Dic:	63	"	"	85	"	"	(8	"	1	")	"
Kap 111 Dic/Ris:	26	"	"	65	"	"	(5	"	1	")	"
San 111 Dic cra:	10	"	"	30	"	"	(3	"	1	")	"
Wal 111 Dic odo:	12	"	"	50	"	"	(> 1	"	1	")	v. rare
Bir 111 Sph 2spp:	47	"	"	550	"	"	(> 1	"	1	")	"
Aas 411 Dic/Sph:	44	"	"	512	"	"	(> 1	"	1	")	"
Umk 111 Dic 2spp:	14	"	"	400	"	"	(1	"	3	")	"
Lit 111 Dic/Hei:	10	"	"	550	"	"	(1	"	5	")	ex. rare

The above nine TCs (of the 18 yielding *Fraxinopsis*) are covered in the photographic plates. For the TCs (Maz 211, Bir 111 and Aas 411) with 30 or more curated individuals, the recorded abundance is conservative as only the better preserved specimens have been retained (see Tab. 64).

Affiliated organs
Male strobilus: unknown.
Foliage: *Yabeiella*—Grade 4 (Cut. cor., Mut. occ.).

Classification & comparison
Suprageneric classification (Fraxinopsiaceae/Fraxinopsiales)
Fraxinopsis shows similarities, as noted by Wieland (1929), to both *Fraxinus* (extant angiosperm) and *Cycadocarpidium* (Triassic pinopsid), but apparently bears no phylogenetic relationship to either. It affiliates repeatedly with the leaf genus *Yabeiella* in South Africa, South America and Australia. *Yabeiella* is a distinctive leaf, with basic taeniopteroid venation, irregular anastomoses and clear marginal vein. It is restricted to the Gondwana Triassic and is entirely unlike that of *Fraxinus* or of *Podozamites* which is affiliated with *Cycadocarpidium*. The venation and cuticular features (And. & And. 1989, p. 472) of *Yabeiella* suggest links with the Gnetopsida. The *Fraxinopsis/Yabeiella* plant, all considered, is placed in the new order Fraxinopsiales and new family Fraxinopsiaceae.



Reconstructions
Only minor reconstruction clarifying venation, auricular lobes or hirsuteness has been attempted in the numerous sketches of the seeds. No information is available on how the seed was attached to the plant.

Gondwana Triassic occurrence (elaborated)

Fraxinopsis is well known and common from three disjunct regions of Gondwana—N. Argentina, the Karoo Basin of South Africa and the Clarence-Moreton Basin, Queensland. It is clearly more frequent and abundant in these regions than is reflected in the hypodigm alone. Jones & De Jersey (1947), for instance, report *Fraxinopsis* (without giving any abundance data) from 10 Ipswich Coalfield localities—Kholo, Tivoli and Cooneana Stages of the Ipswich Series, while Jain & Delevoryas (1967) record 19 specimens in the Wieland collection from the Minas de Petroleo locality, Cacheuta Basin.

South America (N. Argentina)

1929, Wieland: *Fraxinopsis major* and *F. minor*; f5 (a, b); new genus and two species based on *ca* 10–20 specimens, Minas de Petroleo, Cacheuta Basin, N. Argentina; Potrerillos Fm. (Carnian, U. Triassic).

1931, Oishi: *Fraxinopsis minor*, pl. 26(1, 1a); a single specimen from near Minas de Petroleo; Potrerillos Fm.

1941a, Frenguelli: *Cycadocarpidium andium*; pl. 1–3, tf. 1–3; a new species based on five illustrated specimens. Estratos con *Estheria*, Cacheuta Basin; Cacheuta Fm. (Carnian, U. Triassic).

1941b, Frenguelli: repeats after Wieland 1929.

1944b, Frenguelli: *Cycadocarpidium major*, *C. minor* and *C. andium*; pl. 1–4 (*ca* 20 specimens); locality behind old YPF building, Cacheuta Basin; Potrerillos Fm.

1963, Bonetti: *Cycadocarpidium andium*, pl. 39(1–4), pl. 40(1, 2); 6 specimens illustrated; Punto 20, 21, Barreal-Hilario Basin, N. Argentina; Cortaderita Fm. (Carnian, U. Triassic).

1967, Jain & Delevoryas: *Fraxinopsis major* and *F. minor*, pl. 97(9–14), six specimens illustrated, 19 specimens recorded; Minas de Petroleo (site and collection as for Wieland 1929).

1969, Menéndez: *Cycadocarpidium andium*, pl. on p. 535(1); repeat after Frenguelli 1941a.

1995, Ganuza *et al.*: *Cycadocarpidium andium* and *C. majus*, pl. 2(g, h), two specimens illustrated and recorded; Paso Flores region and Fm.; here identified as belonging to *F. cornicordis*.

Australia (Queensland, Clarence-Moreton Basin)

1947, Jones & De Jersey: *Fraxinopsis major*, p. 54, tfs 49, 50; specimens without abundance data from 10 localities, Ipswich Coalfield, Clarence-Moreton Basin, Queensland; Kholo, Tivoli & Cooneana Stages, Ipswich Series (Carnian, U. Triassic).

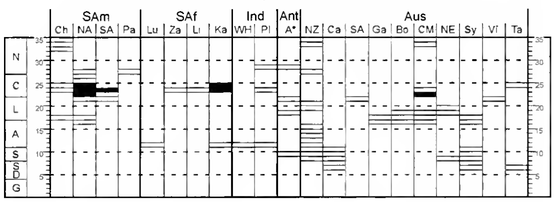
1965, Hill *et al.*: *Fraxinopsis major*, pl. T6(6); a single specimen illustrated from Petrie's Quarry, Albion, Ipswich Coalfield; Tingalpa Fm., Ipswich Series.

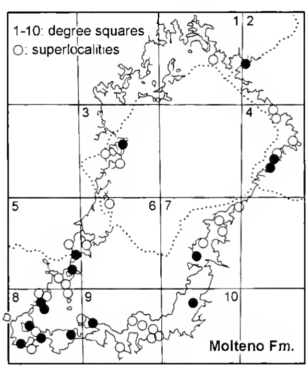
Tab. 63

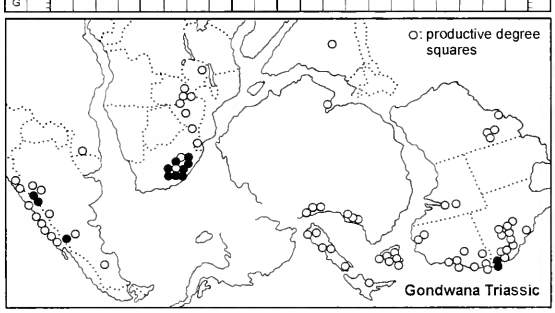
FRAXINOPSIS HYPODIGM, Gondwana Triassic occurrence

AUTHOR		SUBREGION		FORMATION		LOCALITY	NAME	Indivs	ILLUSTRATION	Species: Molteno *F. andium*	*F. auriculatata*	*F. cornicordis*	Other *F. minor*	*F. major*	*F. spp. indet*
SOUTH AMERICA															
1929	Wieland	Cacheuta	NA4	24	Potrerillos	Minas de Petroleo	*Fraxinopsis major*	1	f 5(*a*)	-	-	-	-	1	-
"	"	"	"	"	"	" " "	" *minor*	2	f 5(b)	-	-	-	2	-	-
1931	Oishi	"	"	"	"	" " "	" "	1	pl 26(1,1a)	-	-	-	1	-	-
1941a	Frenguelli	"	"	25	Cacheuta	(Estratos con Estheria)	*Cycadocarpidium andium*	5	pl 1-3, tf 1-3	5	-	-	-	-	-
1941b	" (specimen repeated from Oishi 1931, Frenguelli 1941b)							*							
1944b	"	Cacheuta	NA4	24	Potrerillos	Old YPF admin. Building	*Cycadocarpidium minus*	8	pl 1(1-7), 4(1,2), tf 1A	1	-	-	8	-	-
"	"	"	"	"	"	" "	" *andium*	8	pl 2(1-7), 4(2), 5(1)	8	-	-	-	-	-
"	"	"	"	"	"	" "	" *majus*	5	pl 3(1-5), tf 1B	-	-	-	-	5	-
1963	Bonetti	Barreal	NA2	23	Cortaderita	Punto 20,21	" *andium*	6	pl 39(1-4), 40(1,2)	6	-	-	-	-	-
1967	Jain & Delev.	Cacheuta	NA4	24	Potrerillos	Minas de Petroleo	*Fraxinopsis major*	3	pl 97(9-11)	-	-	-	-	3	-
"	"	"	"	"	"	" "	" *minor*	3	pl 97(12-14)	-	-	-	3	-	-
1969	Menendez (specimen repeated from Frenguelli 1941b)							*							
1995	Ganuza *et al.*	Paso Flores	SA1	24	Paso Flores	El Cañadón de Pancho	" *andium*	1	pl 2(g)	-	-	1	-	-	-
"	"	"	"	"	"	" "	" *majus*	1	pl 2(h)	-	-	1	-	-	-
AUSTRALIA															
1947	Jones & de J.	Ipswich/Esk	CM5	23	Tivoli Stage	Chuwar (locs. 5,6)	*Fraxinopsis major*	2	tf 49,50	-	-	-	-	2	-
1965	Hill *et al.*	Brisbane	CM6	"	Tingalpa Fm.	Petrie's Quarry (Albion)	" "	1	pl T6(6)	-	-	-	-	1	-
SOUTH AFRICA															
1978-1999 And. & And. Molteno literature not included in this table															

GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION







Evidence for affiliation of organs

The link between the foliage genus and the winged seed *Fraxinopsis* is virtually certain (Grade 4 reliability) short of organic attachment. This is based on repeated *mutual occurrence* on three Gondwana continents—South Africa, South America and Australia—and on the close similarity of their characteristic cuticle. Meanwhile, the male affiliate of *Yabeiella* remains unknown.

Mutual occurrence

South Africa—*Fraxinopsis* is known from 18 of the 100 Molteno TCs studied (Tab. 64). In the majority of cases (14 of 18) it occurs with *Yabeiella*, which is known from a total of 29 TCs. At least three of the four TCs (Bir 211, Bir 311 and Mol 111) with *Fraxinopsis*, but no *Yabeiella*, would very likely yield the latter on more comprehensive sampling. These three TCs all represent floodplain lake deposits dominated by the foliage genus *Sphenobaiera*, as do the very well-sampled sites, Bir 111 and Aas 411, that have yielded *Yabeiella* fairly commonly along with *Fraxinopsis* (Tab. 64).

At the remaining TCs where *Yabeiella* is very rare, it is not surprising that *Fraxinopsis* has not been found. However, there are four TCs where *Yabeiella* is fairly common (1% of the total flora at Nav 111, Kon 111, Kon 222 and Hla 213) but no *Fraxinopsis* has been found. Three of these TCs occur in *Dicroidium* open woodland habitats (Tab. 64).

South America—The genera *Fraxinopsis* and *Yabeiella* are clear affiliates at five of the six North Argentinean localities (Tab. 63) yielding the winged seed.

Australia—Jones & De Jersey (1947) make special note of the 'constant association' of *Fraxinopsis* and *Yabeiella*: 'In the Ipswich Series *Fraxinopsis* has only been found at localities at which species of *Yabeiella* occur'.

Cuticular correspondence

The cuticle of *Yabeiella* (p. 377, tfs 11, 12) and *Fraxinopsis*, with the deeply sinuous cell walls and narrowly elliptic guard cells, is essentially identical and quite distinct from other Molteno plants.

Cuticles

Potential sample: Lit 111, 10 indivs; Umk 111, 12 indivs.
Macerated (this work): Lit 111, no results from three macerations (but two peels from wing area productive).
Preservation grade: Grade 3 (fair), some features present, large pieces.
Diagnostic characters: cells amorphous, walls meandering, nonpapillate; stomata interveinal (whether adaxial or abaxial unknown), orientation longitudo-random; subsidiary cells anomocytic, noncutinised; guard cells narrowly elliptic.
Comment: A distinctive feature is the elongate hairs visible along the wing margin.
Significance:
Classification—See notes on pp. 370, 376.
Affiliations—The cuticle unequivocally supports the affiliation already suggested by the repeated mutual occurrence of *Fraxinopsis* and *Yabeiella*.

Species nomenclature in Fraxinopsis

The particular problem encountered here in applying South American *Fraxinopsis* names to Molteno material revolves around the difficult taxonomy/nomenclature relationship (see Hypodigm, Tab. 63).

Weiland (1929) described *Fraxinopsis minor* and *F. major* based on an undisclosed number of specimens from the single Minas de Petroleo locality, Potrerillos Fm., Cacheuta Basin. The *F. minor* holotype measures 24 mm in length and shows largely parallel venation, while the *F. major* holotype is 30 mm long with more spreading dichotomous venation. The former species was apparently the more abundant.

From our understanding of over 250 *Fraxinopsis* specimens from 18 Molteno TCs, only one palaeodeme occurs at any one site and each shows a marked range of morphological variation. This pattern may apply also to the South American material. Jain & Delevoryas (1967) illustrated a further three specimens of each species from the original Minas de Petroleo locality, but provided no information on their spread of variation. This is a critical point. If the collection does indeed represent a single palaeodeme with a continuous range of variation in size, then *F. major* and *F minor* represent a single species.

F. andium, described by Frenguelli (1941a), includes the holotype with a length of 18 mm and the four additional illustrated specimens of similar size (18–20 mm). The common and variable Molteno species (from 16 TCs) has a size range of *ca* 9 mm to a maximum of 24 mm. The Bir 111 reference palaeodeme ranges from *ca* 12–20 mm. The two additional species from the Molteno, *F. auriculata* and *F. cornicordis*, are clearly distinct and range upwards from 32 mm in length.

We place our common Molteno species in *F. andium* and recognise *F. minor* and *F. major* as distinct species until further studies are undertaken on the South American material. The two specimens described by Ganuza *et al.* (1995) as *F. andium* and *F. majus*, with lengths of 39 and 45 mm respectively, are here both identified as *F. cornicordis*.

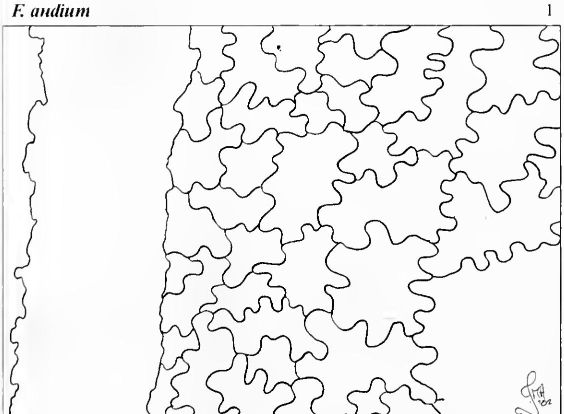
Adaptive radiation (Molteno diversity)

Palaeodemes of the foliage genus *Yabeiella* often show a good deal of variation and it is difficult to demarcate species. A similar situation is encountered in the winged seed genus *Fraxinopsis*, where considerable intra- and interpalaeodeme variation occurs. Of the 18 Molteno palaeodemes (each from a different TC), only two are clearly distinct from the rest and are recognised as separate species. The majority (16 TCs) fall into *F. andium* originally described from Argentina.

The three species are distinguished on the basis of size, wing venation, hirsuteness and shape of seed head. They are based on the following TCs/reference palaeodemes, all of which occur in floodplain deposits:

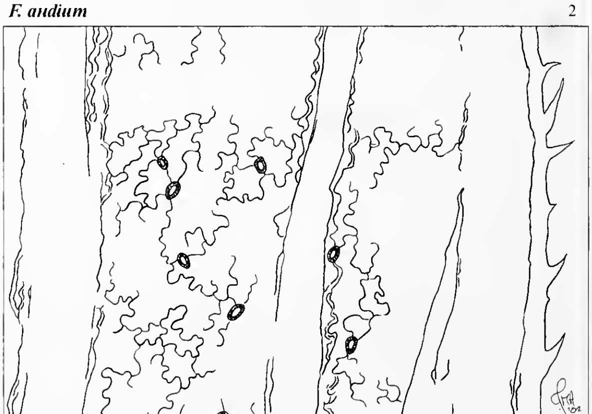
F. andium—Bir 111 Sph 2spp, (Birds River); 47 indivs
Sphenobaiera closed woodland (floodplain lake); Cycle 5 (Tsomo Member)
F. auriculata—Wal 111 Dic odo, (Waldeck); 12 indivs
Sphenobaiera closed woodland (floodplain lake); Cycle 2 or 3 (Indwe & Mayaputi Member)
F. cornicordis—Kra 311 Dic odo (Kraai River); 35 indivs
Dicroidium open woodland (floodplain); Cycle 3 (Mayaputi Member)

F. andium 1



upper **Lit 111** BP/2/2200 x250

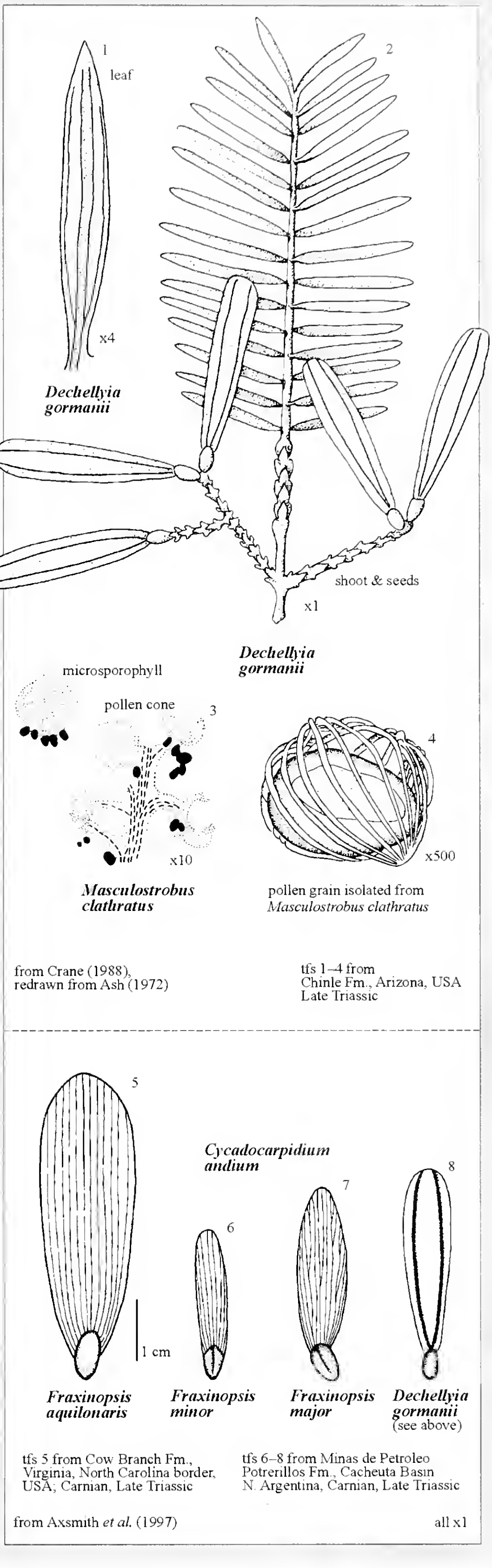
F. andium 2



lower **Lit 111** BP/2/2200 x100

assemblages (taphocoenosis)		Genera: *Yabeiella*	Genera: ♀*Fraxinopsis*	Species: *F. andium*	Species: *F. auriculata*	Species: *F. cornicordis*	Molteno Cycles
Nav 111	Dic odo	**1**	-	-	-	-	5
Bir 211	Sph 2spp	-	1	1	-	-	
" 311	Hei/Sph	-	5	5	-	-	
" 111	Sph 2spp	40	47	47	-	-	
Gre 111	Equ sp.	1	1	1	-	-	4/5
Boe 111	Lep sto	5	-	-	-	-	
" "	Dic/Hei	1	1	1	-	-	
Mol 111	Sph pon	-	2	2	-	-	
Ela 111	Dic odo	6	-	-	-	-	3
Kra 311	" "	18	35	-	-	35	
Lut 311	Hei elo	9	6	6	-	-	
" 211	Sph pon	4	-	-	-	-	
Tin 121	Sph 2spp	1	1	1	-	-	
Wal 111	Dic odo	20	12	-	12	-	2/3
Kon 223	" "	1	-	-	-	-	2f
" 222	" "	**1**	-	-	-	-	
" 211	Ast 2ssp	1	-	-	-	-	
" 111	Dic odo	**1**	-	-	-	-	
Pen 321	Dic/Ris	2	-	-	-	-	
Kle 111	Hei/Dic	-	1	1	-	-	
Kap 111	Dic/Ris	5	26	26	-	-	2e
Qua 111	Dic odo	5	-	-	-	-	2c
Maz 111	Dic cra	22	27	27	-	-	
" 211	Dic/Hei	11	63	63	-	-	
Hla 211	Dic 3spp	1	-	-	-	-	2b
" 213	Dic elo	**1**	-	-	-	-	
Umk 111	Dic 2spp	45	14	14	-	-	
Inj 111	Dic odo	2	-	-	-	-	
San 111	Dic cra	**2**	10	10	-	-	
Mat 111	Dic/Hei	2	-	-	-	-	
Lit 111	Dic odo	6	10	10	-	-	2a
Aas 411	Dic/Sph	60	44	44	-	-	1
" 511	Dic elo	1	-	-	-	-	
Total TCs		29	18	16	1	1	
Total indivs		%	306	259	12	35	

Tab. 64. *Fraxinopsis/Yabeiella*, Molteno occurrence



Beyond Gondwana Triassic

Laurasian Triassic: *Dechellyia* (tfs 1, 2 adjacent), a winged seed attached to the foliage of the same name, from the Late Triassic of southwestern United States (Ash 1972), is somewhat similar but differs in lacking a groove on the seed body and in the two veins or thick ribs that nearly converge in the wing base. *Cycadocarpidium*, which is widespread in Laurasia, is superficially similar to *Fraxinopsis* but is known to be a conifer scale belonging to the Voltziales (And. & And. 1989, p. 423; Axsmith *et al.* 1997, p. 304).

Fraxinopsis has recently been recorded from the Late Triassic of eastern United States (Axsmith *et al.* 1997). Their *F. aquilonaris* (tf. 5 adjacent) is similar to Gondwana *Fraxinopsis* species but differs in lacking a groove along the seed body and in the absence of any forking or anastomoses in the wing venation. *Yabeiella* does not occur in association with *F. aquilonaris* and no other affiliated leaf has been suggested. It is most probable that the USA species should be placed in a separate genus.

Other ages: Wieland (1929) originally compared *Fraxinopsis* with the winged seeds of the extant angiosperm *Fraxinus* and suggested that the seed had two cotyledons. However, there is no support for this view (Oishi 1931).

Fraxinopsis andium (Freng. 1941a) J.M.And. & H.M.And., comb. nov.

Holotype
Specimen: 4755 Mus. de la Plata, Argentina; Frenguelli [1941b, pl. 1(1, 2)].
Assemblage: Estratos con *Estheria*, Cacheuta Basin, N. Argentina; Cacheuta Fm., Carnian.
Preservation: virtually complete seed; part and counterpart.

Reference palaeodeme
Assemblage (TC): Bir 111 Sph 2spp, Molteno Fm.
Specimens: 47 indivs; pl. 144(1–10).

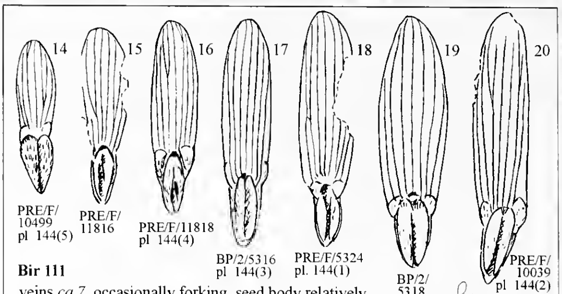
Sister palaeodemes—15 (best 6 listed)
Kap 111 Dic/Ris: 26 indivs; fine preservation.
San 111 Dic cra: 10 indivs; fine preservation.
Umk 111 Dic 2spp: 14 indivs; with cuticle.
Lit 111 Dic/Hei: 10 indivs; with cuticle, clear hairs.
Maz 211 Hei/Dic: 63 indivs; clear hairs & preservation.
Maz 111 Dic cra: 27 indivs; comparative full palaeodeme.

Specific diagnosis
A *Fraxinopsis* species of small size, with a wing showing *ca* 7 simple to occasionally forking veins, and hirsute seed body with small auricles.

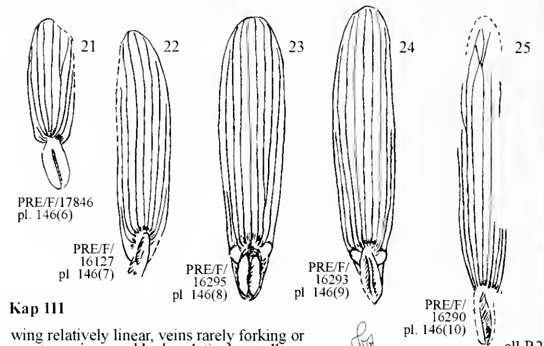
Specific characters
Seed: small (*ca* 12–21 mm long); wing partially hirsute, veins *ca* 7 at widest point, occasionally forking, rarely anastomosing; seed body distinctly hirsute, relatively large ($^1/_3$–$^1/_2$ length of wing), with small lateral auricles.

Etymology
andium—the name given by Frenguelli (1941a), probably referring to the Andes Mountains.

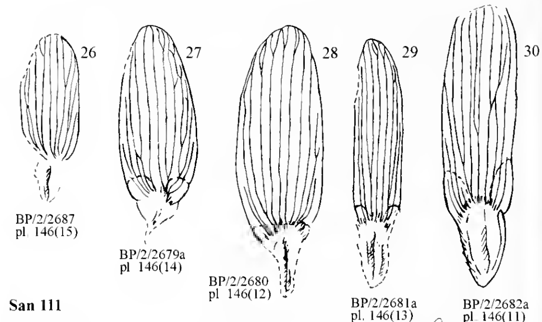
Comment & comparison
This species, as recorded from 16 Molteno TCs, is particularly variable, both within and between palaeodemes. The seven best sampled of the 16 palaeodemes are illustrated here to show this intraspecific diversity. Each palaeodeme is quite distinctive and each probably merits subspecific status—some might merit species status—but the morphological distance between them is far less than that which separates out the species *F. auriculata* and *F. cornicordis*. The most diagnostic features of the seven palaeodemes are noted under the line illustrations.



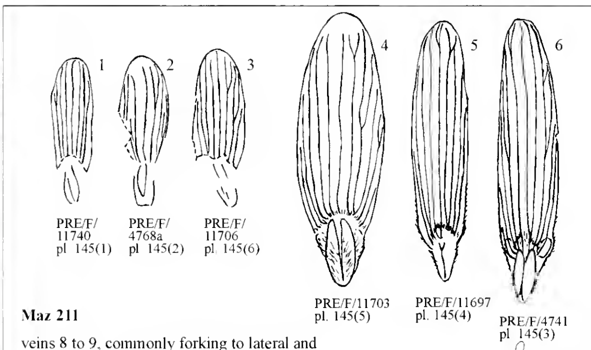
Bir 111
veins *ca 7*, occasionally forking, seed body relatively large, seed body and wing distinctly hirsute



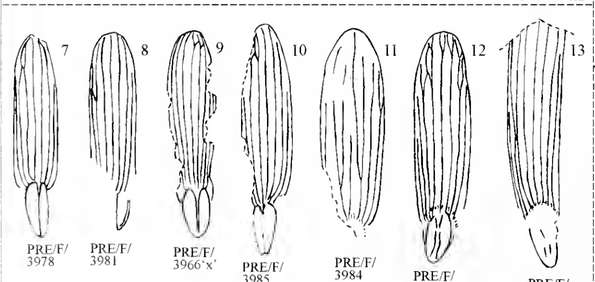
Kap 111
wing relatively linear, veins rarely forking or anastomosing, seed body relatively small



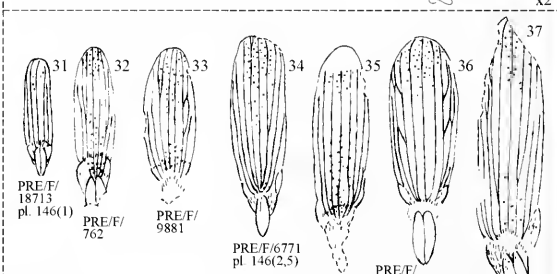
San 111
wing relatively oval, veins commonly forking or anastomosing, seed body relatively large



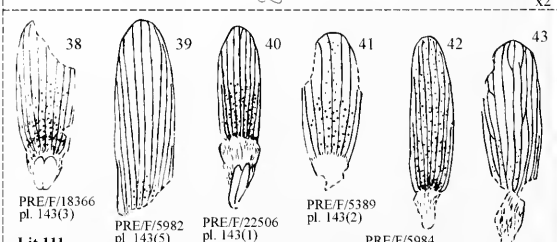
Maz 211
veins 8 to 9, commonly forking to lateral and distal margins, seed body and wing margins distinctly hirsute.



Maz 111
wing relatively linear, veins commonly anastomosing around distal margin



Umk 111
wing with hair bases in proximal and distal concentrations



Lit 111
wing with hair bases confined to proximal concentration, seed body densely hirsute

Fraxinopsis auriculata J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/9408, pl. 147(5).
Assemblage: Wal 111 Dic odo, Waldeck.
Preservation: virtually complete seed, no counterpart; impression in thickly laminated, moderately baked, medium light grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 12 indivs; pl. 147(1–9).

Sister palaeodeme—nil.

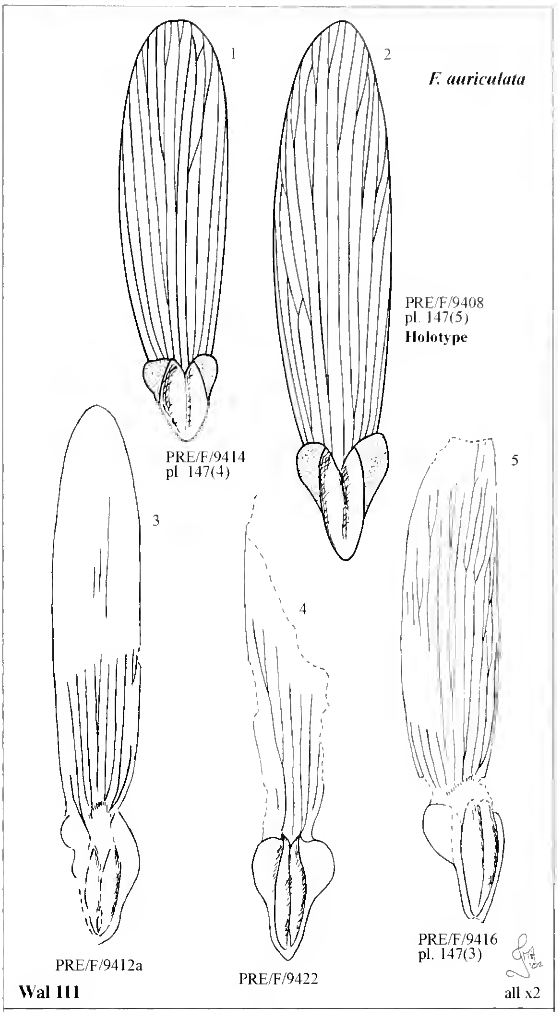
Specific diagnosis
A *Fraxinopsis* species of medium size, with a wing showing *ca* 10 forking and anastomosing veins, and glabrous seed body with well-developed lateral auricles.

Specific characters
Seed: medium (*ca* 32–42 mm long); wing glabrous, veins *ca* 10 at widest point, commonly forking, often anastomosing towards apex; seed body glabrous, medium ($^1/_4$ length of wing), with well-developed lateral auricles.

Etymology
auriculata—auricula (Lat.), ear; with reference to the diagnostic auricles.

Comment & comparison
F. auriculata, known only from the single palaeodeme (12 individuals) from Waldeck (Wal 111), differs from the other species in the large protruding auricles which are consistently developed. *F. andium* has much smaller auricles.

The function of the auricles is not understood. They appear not to be present in any other plant group with winged seeds.



Fraxinopsis cornicordis J.M.And. & H.M.And., sp. nov.

Holotype
Specimen: PRE/F/8225; pl. 148(2, 4, 6).
Assemblage: Kra 311 Dic odo, Kraai River.
Preservation: virtually complete seed, part and counterpart; impression in very thin-bedded, medium grey cherty shale with moderate cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 35 indivs; pl. 148 (1–6).

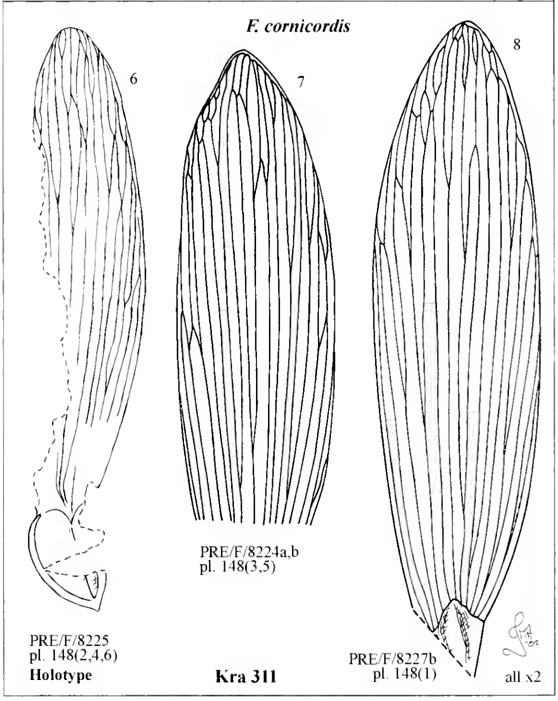
Sister palaeodeme—nil.

Specific diagnosis
A *Fraxinopsis* species of large size, with a wing showing *ca* 16 frequently anastomosing veins, and glabrous seed body without auricles.

Specific characters
Ovule/seed: large (up to >50 mm long); wing glabrous, veins *ca* 16 at widest point, commonly forking, frequently anastomosing towards apex; seed body glabrous, relatively small ($^1/_5$ length of wing), without auricles.

Etymology
cornicordis—cornix (Lat.), crow; *cordis* (Lat.), heart; with reference to the type locality and the shape of the seed body.

Comment & comparison
F. cornicordis is represented by the single palaeodeme of 35 individuals from Kraai River (Kra 311). It is larger in size than *F. auriculata*, and differs in the lack of auricles. It differs from the remaining species in its large size and frequently anastomosing veins. Ganuza *et al.* (1995) illustrated two specimens from Argentina which are tentatively placed in this species based on their large size.



Yabeiella Oishi 1931

Type species

Yabeiella brackebuschiana (Kurtz) Oishi 1931.
Cacheuta, N. Argentina; Carnian, Triassic.

Generic concept

A stem-gnetopsid leaf of linear to narrowly elliptic shape, with entire lamina and occasionally to frequently anastomosing taeniopteroid venation ending at an intramarginal vein.

Generic characters

Leaf: small to medium, linear to narrowly elliptic; lamina undivided, entire, tip roundly obtuse to retuse, base cuneate to attenuate, without distinct petiole; venation taeniopteroid, closely to well spaced, extending at *ca* 20–30° from horizontal, forking to repeatedly anastomosing, with intramarginal vein.
Cuticle: see And. & And. (1989, p. 472); and this vol., tfs 11, 12 opposite.

Eponymy

Yabiella—named by Oishi (1931) in honour of Prof. H. Yabe.

Global range: 2 spp., Gondwana, Tr. (LAD–NOR).
First: *Yabeiella* sp. (Webb 1980); UQL.4255, Esk Fm., Ipswich/Esk, Queensland, Australia.
Last: *Yabeiella* sp. (Webb 1980); UQL.4259, Woogaroo Fm., Brisbane, Queensland, Australia.

Gondwana Triassic occurrence

Frequency (F): 21 degree squares (of the 84 across Gondwana).
Ubiquity (U): 3 continents (of 5 comprising Gondwana).
Diversity (D): 2 foliage species.
Abundance (A): <1% (the norm as in Molteno TCs).
Longevity (L): 17 myrs (early Ladinian to later Norian).

Colonisation success: FUDAL rating—21/3/2/–/17 = 43.
Intermediate success (Grade 3): *Yabeiella* was the 10th most prominent Gondwana Triassic genus; it was frequent, ubiquitous and relatively long-lived, but of low diversity and abundance.
Endemism: both described species (*Y. brackebuschiana* and *Y. mareyesiaca*) are widespread.

Molteno occurrence

Frequency (F): 29 TCs (of 100 sampled in the Molteno).
Diversity (D): 2 species.
Abundance (A): occasional (1–2%) in 5 TCs; rare to very rare (<1%) in the other 24 TCs.

Habit: probably a medium-sized tree.
Preferred habitat: ubiquitous in *Dicroidium* riparian forest and closed woodland of the lake margins; far less frequent in *Dicroidium* open woodland (10 of 31 TCs).

Affiliated organs

Female strobilus: unknown.
Seed: *Fraxinopsis*—Grade 4 (Cut. cor., Mut. occ.).
Male strobilus: unknown.

Classification & comparison

Intergeneric comparison

Gondwana Triassic gymnosperm genera—*Yabeiella* has a number of microfloral features in common with *Jungites* and *Gontriglossa*. They have remarkably similar cuticle with amorphously shaped nonpapillate cells with meandering walls. In megafloral features they are quite distinct: *Yabeiella* having a marginal vein and few anastomoses, *Gontriglossa* strongly anastomosing venation, and *Jungites* occasional anastomoses and an incised lamina margin.

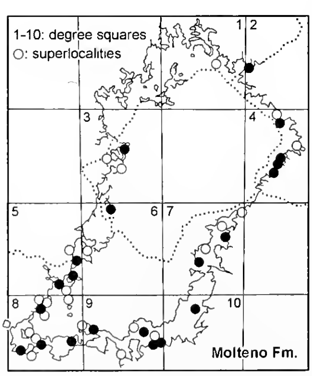
Other genera—We are unaware of any other genera with marginal veins that might be confused with *Yabeiella*.

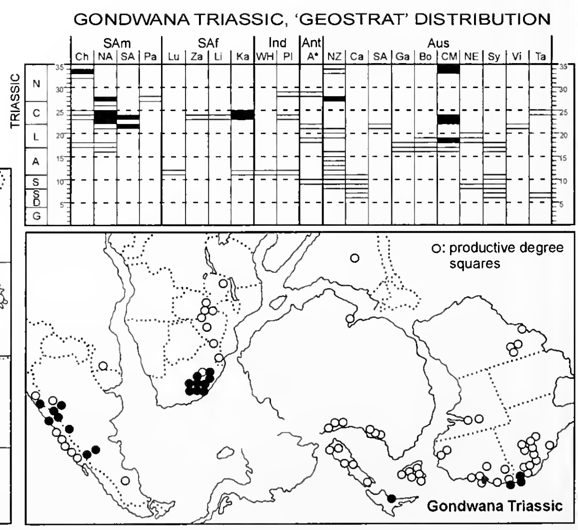
Interspecific comparison

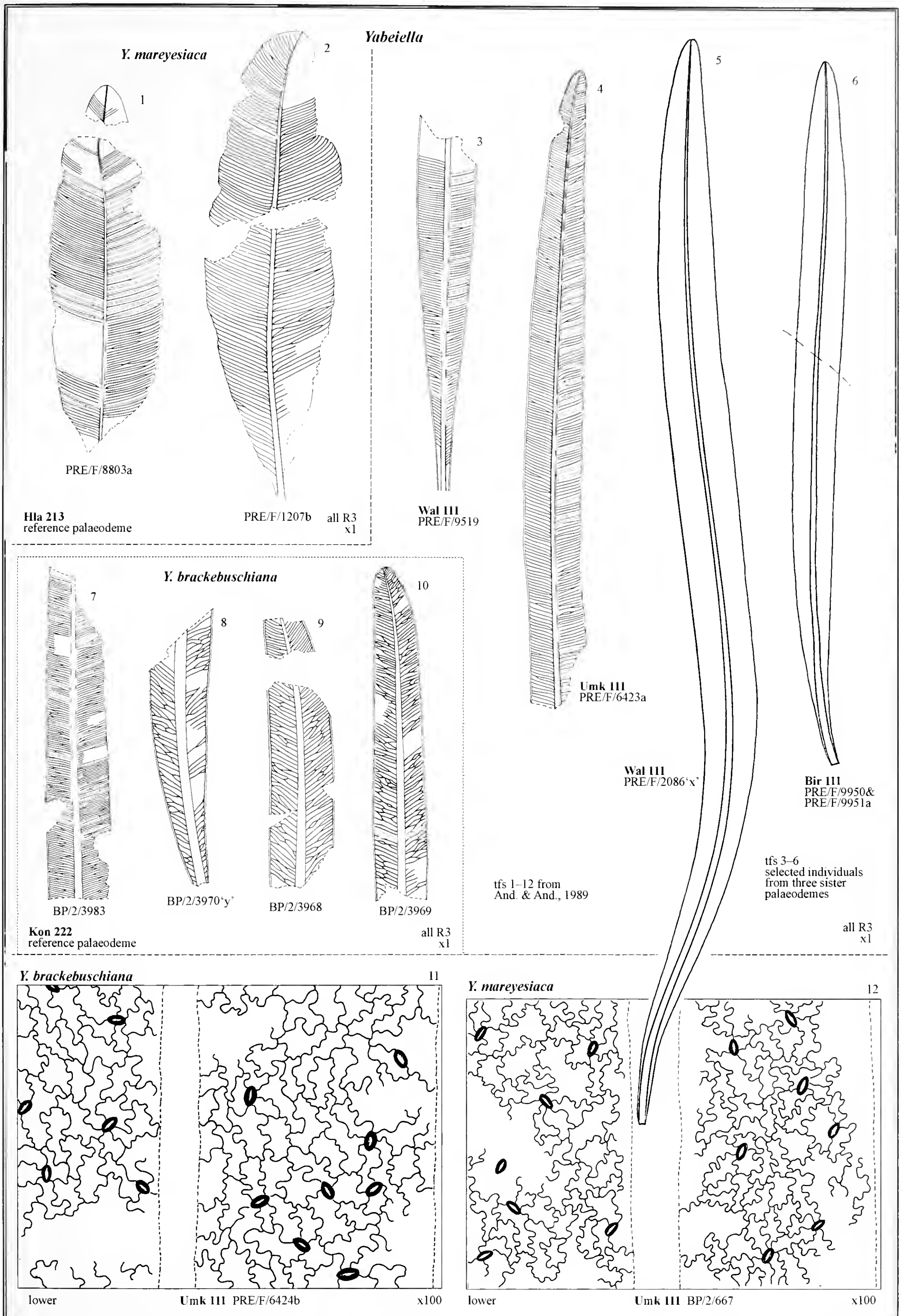
If judged purely on the basis of their leaf macromorphology, the two species of *Yabeiella* recognised here from the Gondwana Triassic might be considered separate genera. However, the fair quality cuticle that has been prepared from both species is more or less identical (And. & And. 1989).

In the Molteno and across Gondwana, the co-occurrence (affiliation) between the leaf genus *Yabeiella* and the seed genus *Fraxinopsis* has been firmly established; but on present evidence we are unable to propose links at specific level.

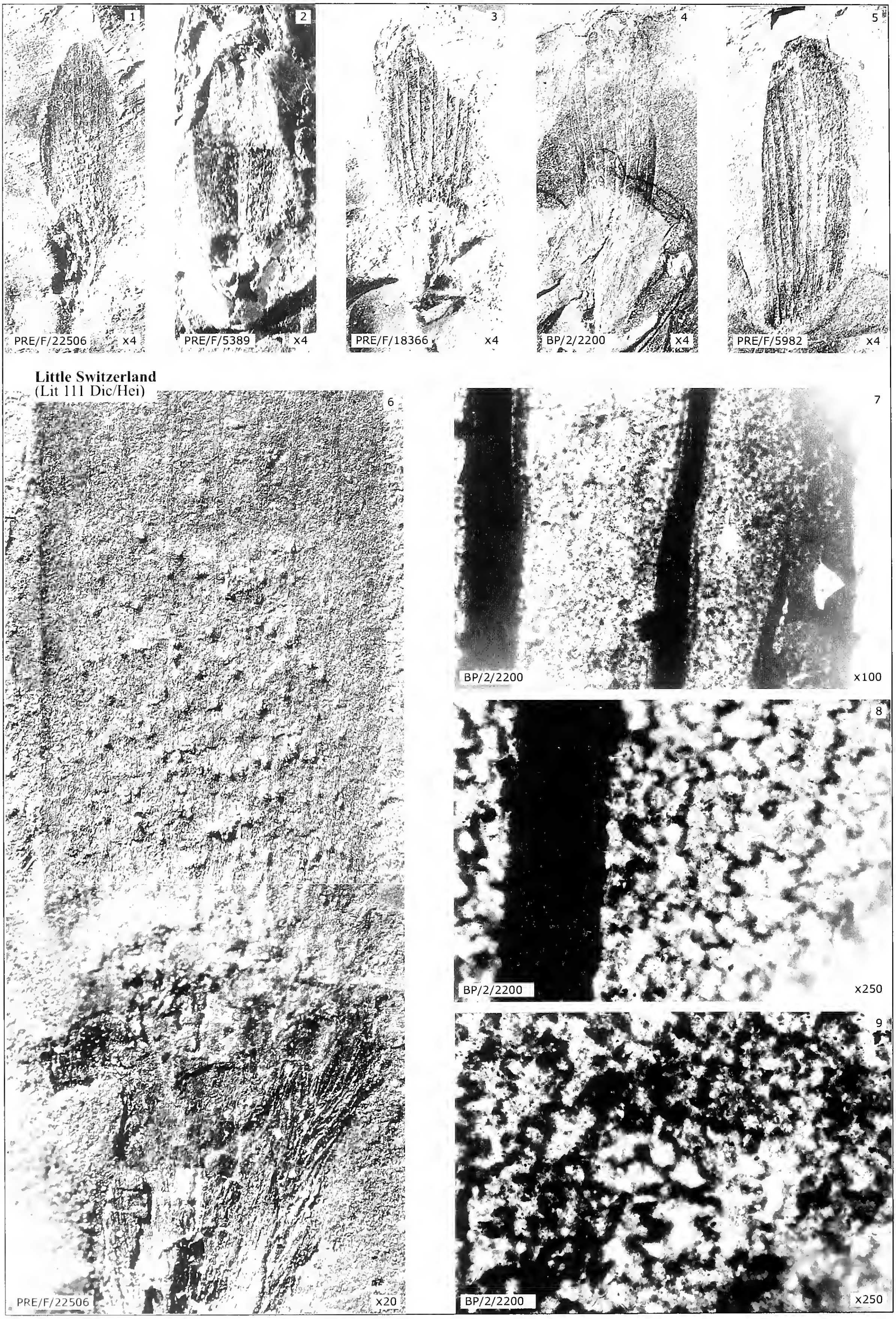
The reference palaeodemes of the two species do not overlap. The full set of 29 palaeodemes of *Y. brackebuschiana* and three of *Y. mareyesiaca* from the Molteno Fm. show no intermediates between the two species, although they occur together at Lut 211, Umk 111 and Aas 411.



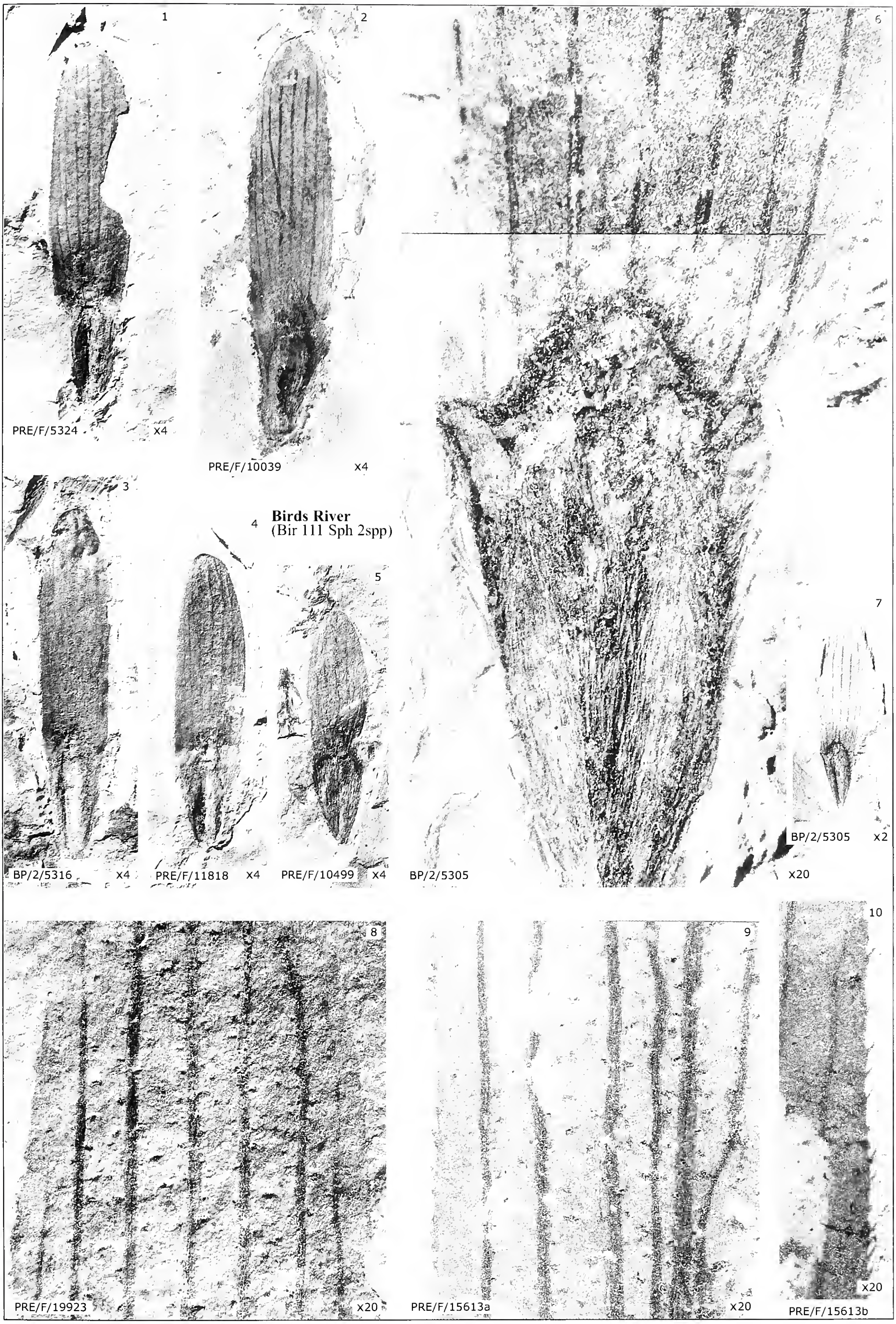




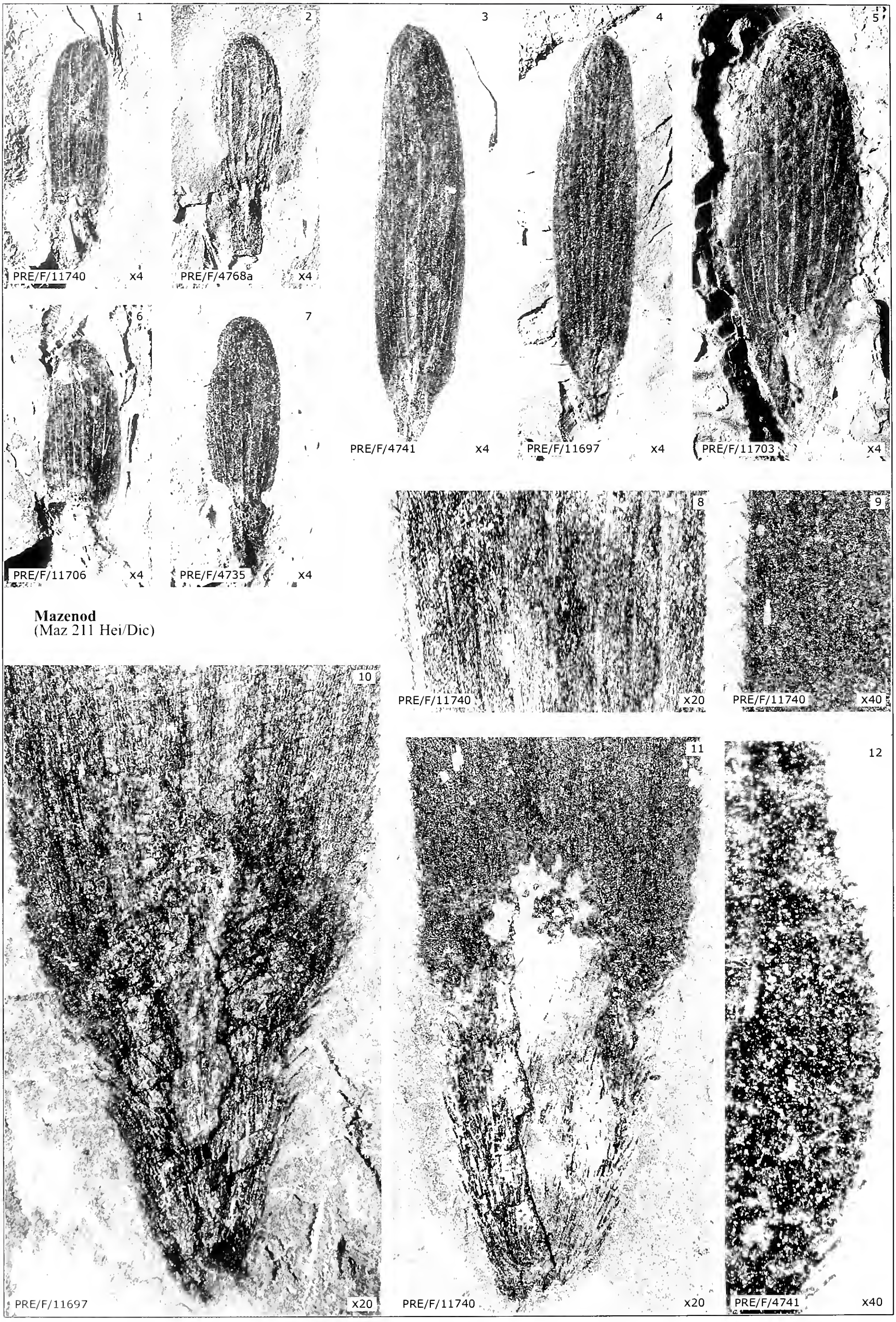
Yabeiella
Y. mareyesiaca
1
2
PRE/F/8803a
Hla 213
reference palaeodeme
PRE/F/1207b
all R3
x1
3
4
5
6
Wal 111
PRE/F/9519
Umk 111
PRE/F/6423a
Wal 111
PRE/F/2086'x'
Bir 111
PRE/F/9950&
PRE/F/9951a
Y. brackebuschiana
7
8
9
10
BP/2/3983
BP/2/3970'y'
BP/2/3968
BP/2/3969
Kon 222
reference palaeodeme
all R3
x1
tfs 1–12 from
And. & And., 1989
tfs 3–6
selected individuals
from three sister
palaeodemes
all R3
x1
Y. brackebuschiana
11
lower
Umk 111 PRE/F/6424b
x100
Y. mareyesiaca
12
lower
Umk 111 BP/2/667
x100



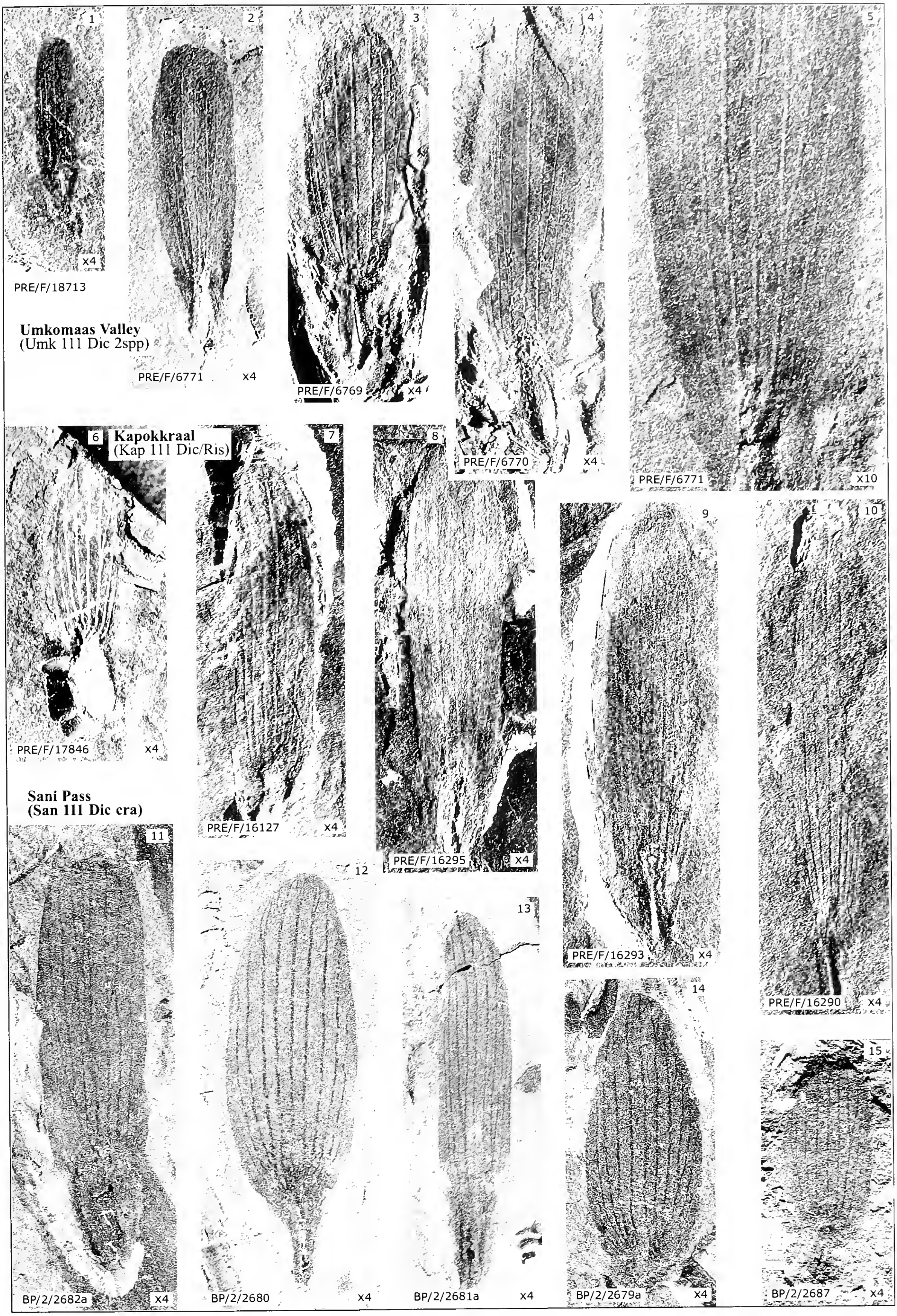
Fraxinopsis andium **pl. 143** **FRAXINOPSIALES**



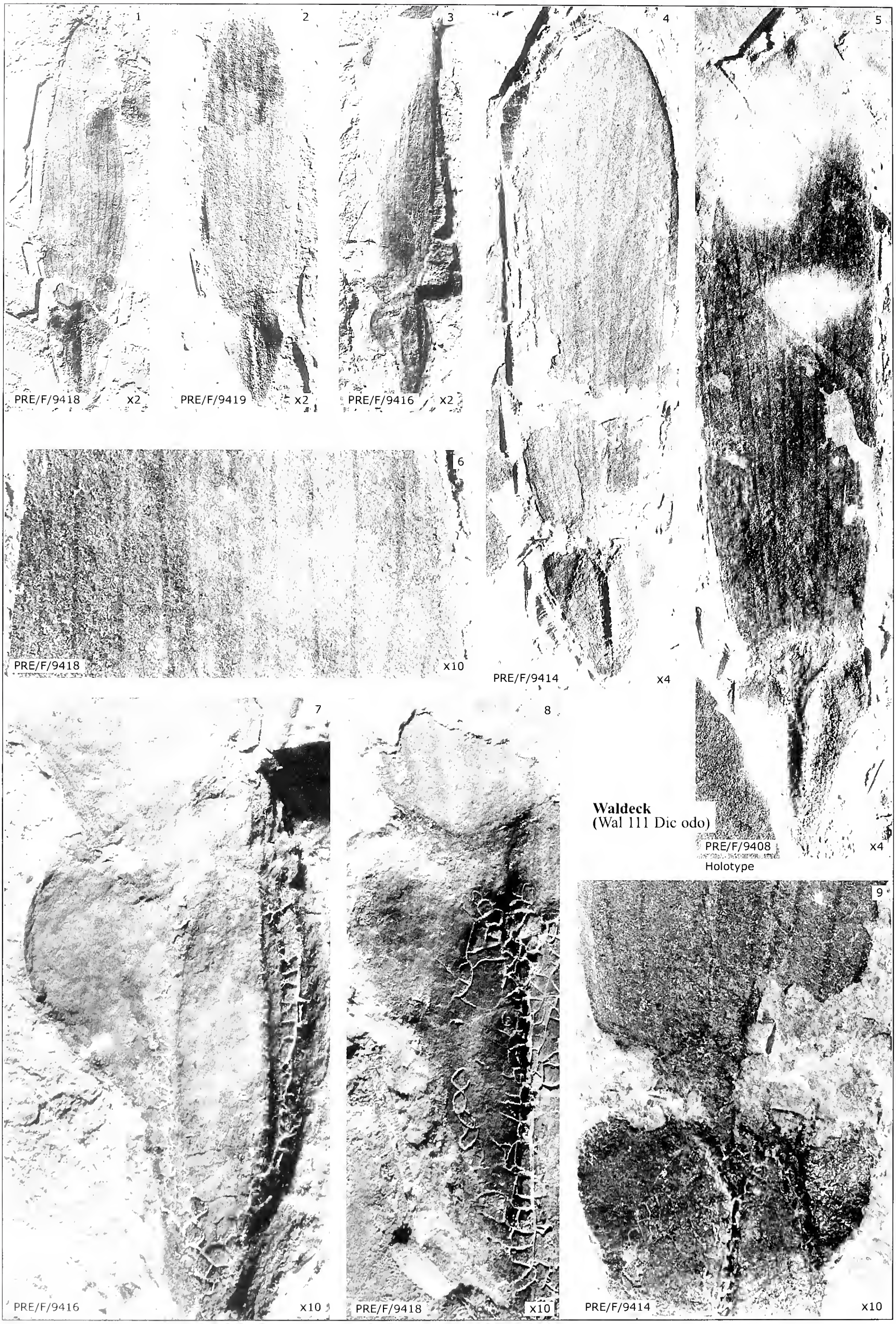
FRAXINOPSIALES pl. 144 *Fraxinopsis andium*

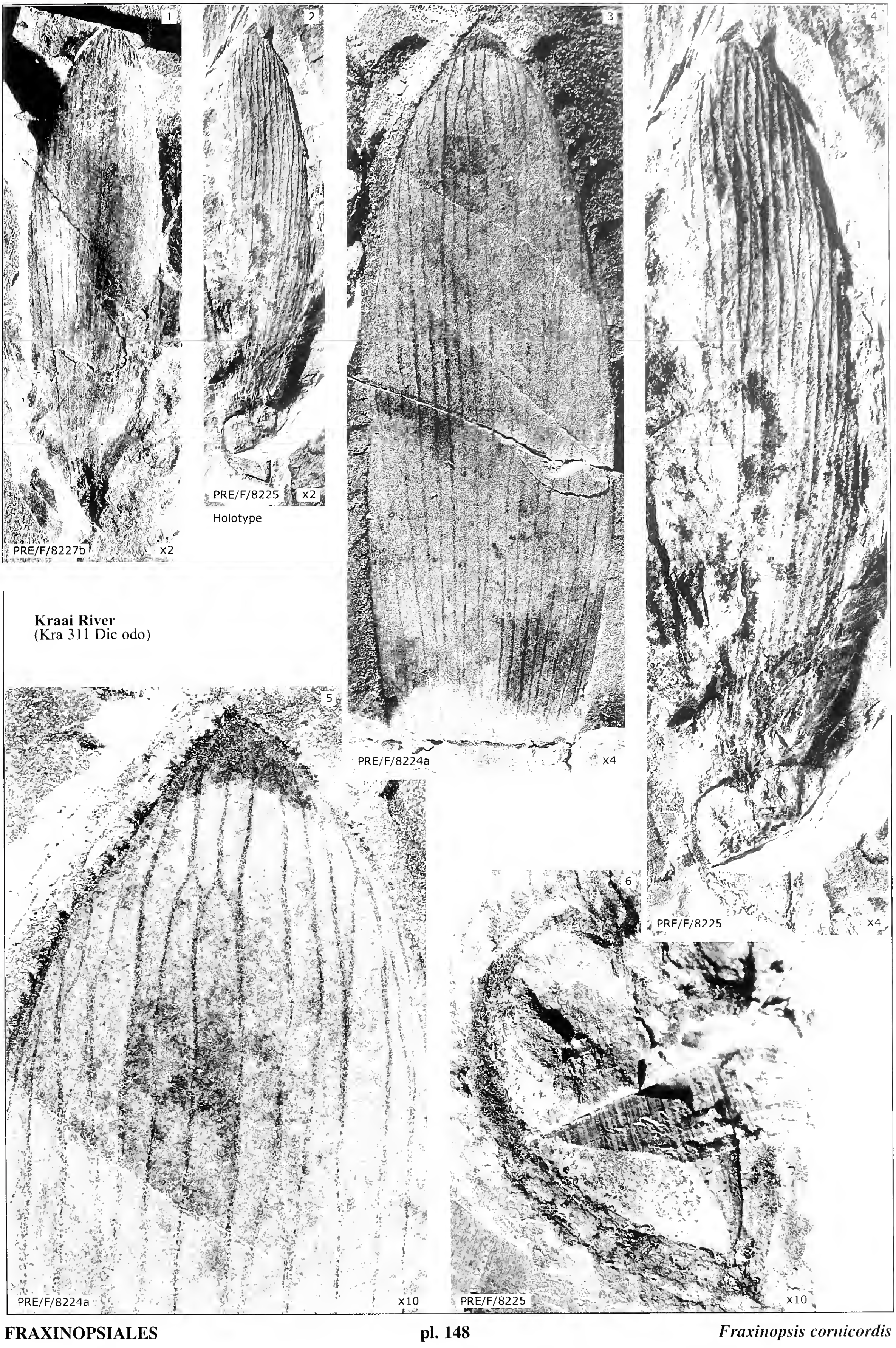


Mazenod
(Maz 211 Hei/Dic)



FRAXINOPSIALES pl. 146 *Fraxinopsis andium*


1
PRE/F/9418 x2
2
PRE/F/9419 x2
3
PRE/F/9416 x2
4
PRE/F/9414 x4
5
PRE/F/9408 x4
Holotype
6
PRE/F/9418 x10
7
PRE/F/9416 x10
8
PRE/F/9418 x10
9
PRE/F/9414 x10
Waldeck
(Wal 111 Dic odo)



FRAXINOPSIALES **pl. 148** ***Fraxinopsis cornicordis***

Jungites J.M.And. & H.M.And. 1989

Type species
Jungites polymorpha J.M.And. & H.M.And. 1989.
Little Switzerland, Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis
A stem-gnetopsid leaf of narrowly to broadly elliptic shape, with irregularly cleft lamina and taeniopteroid venation with occasional anastomoses.

Generic characters
Attachment: fascicle of several leaves on (?)short shoot.
Leaf: small to relatively large, narrowly to (?)broadly elliptic; lamina irregularly and variously cleft, margin very finely irregularly serrulate; tip acute to obtuse; base cuneate to attenuate, without distinct petiole; venation taeniopteroid, closely to well spaced, extending at low angle from horizontal, occasionally forking and anastomosing.
Cuticle: see And. & And. (1989, p. 497); this vol., tfs 4, 6 opposite.

Eponymy
Jungites—for Carl Jung, Swiss psychiatrist with a particular interest in schizophrenia (split personality). The diagnostic feature of the leaf *Jungites* is the irregularly cleft lamina.

Global range: 3 spp., Gondwana, M.–U.Tr. (AWS–CRN).
First: *J. reservoirensis* And. & And. (1989), Burgersdorp Fm., Reservoir, Aliwal North.
Last: *J. polymorpha*, Molteno Fm.

Gondwana Triassic occurrence
Frequency (F): 3 degree squares (of the 84 across Gondwana).
Ubiquity (U): 2 continents (of 5 comprising Gondwana).
Diversity (D): 3 foliage species.
Abundance (A): <1% (the norm in Molteno TCs).
Longevity (L): 13 myrs.

Colonisation success: FUDAL rating 3/2/3/–/13 = 21.
Limited success (Grade 2): *Jungites* was the 17th most prominent genus in the Gondwana Triassic; it was relatively long-lived, but of low frequency, ubiquity, diversity and abundance.
Endemism: all 3 species are single-assemblage endemics.

Molteno occurrence
Frequency (F): 1 TC (of 100 sampled in the Molteno).
Diversity (D): 2 species.
Abundance (A): very rare (<1%) in the single TC.

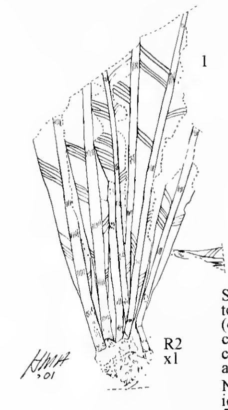
Affiliated organs: unknown.

Classification & comparison
Intergeneric comparisons
Gondwana Triassic gymnosperm genera—As noted earlier, *Jungites* has a range of cuticular features suggesting an obvious relationship with *Yabeiella* and *Gontriglossa* (for further comment on the similarities and differences between the three genera, see text under *Yabeiella*, p. 376).

Other genera—Had *Jungites* not yielded cuticle, we might have included the component species in the cycad genus *Nilssonia* or in one of the cycadeoid genera *Nilssoniopteris* or *Anomozamites*. *Nilssonia* and *Nilssoniopteris* have entire to irregularly divided laminae similar to *Jungites*, while some species of *Nilssoniopteris* and *Anomozamites* also resemble it with their irregularly serrulate margins. The cuticle of *Jungites*, however, is quite unlike that in any cycad or cycadeoid and separates it from those genera.

Interspecific comparisons
The three species of *Jungites* recognised here from the Gondwana Triassic are perfectly distinct, though superficially similar in leaf macromorphology and fall reasonably within the compass of a natural genus. Fair quality cuticle has been derived from both Molteno species, *J. polymorpha* and *J. sp.*A, and proved to be virtually identical. The third species, *J. reservoirensis*, recorded from the early Middle Triassic Burgersdorp Fm. of the Karoo Basin, is from a site without cuticle (And. & And. 1989). A further species possibly occurs in South America (Menéndez 1951), but the two recorded individuals were included as sp. indet. in our earlier revision (And. & And. 1989).

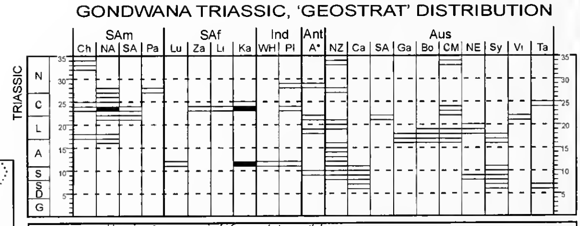
J. polymorpha

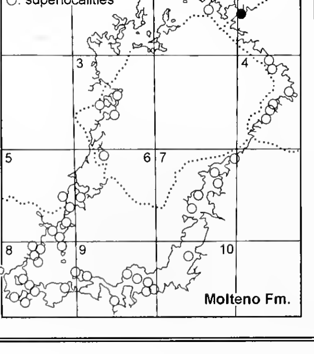


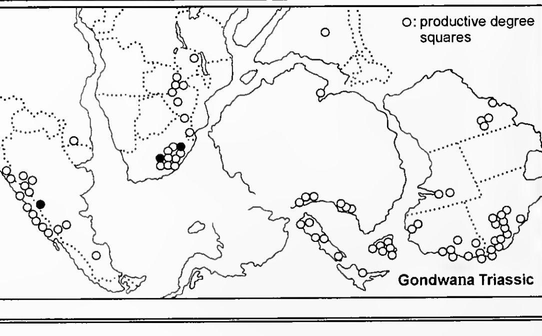
Showing a fascicle of seven leaves attached to a stem. A further two incomplete leaves (one seen here) are lying at right angles and close to the fascicle. The midribs have characteristic markings (?lenticles) that are also present on other *Jungites* leaves.
Note that this specimen was previously identified by And. & And. (1989, pl. 228, tf. 5) as *Taeniopteris cetilocus*.

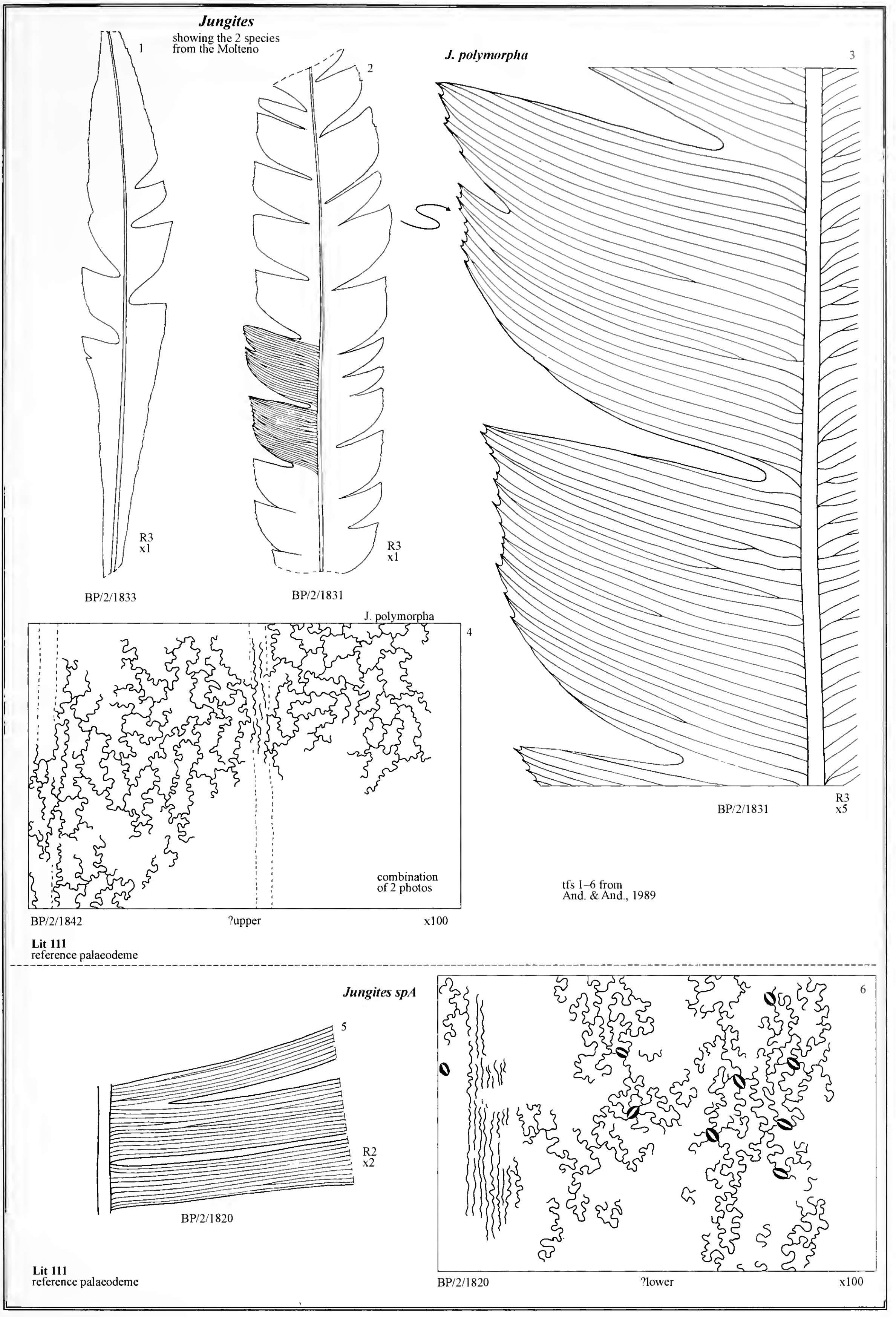
Lit 111 BP/2/1702

GONDWANA TRIASSIC, 'GEOSTRAT' DISTRIBUTION

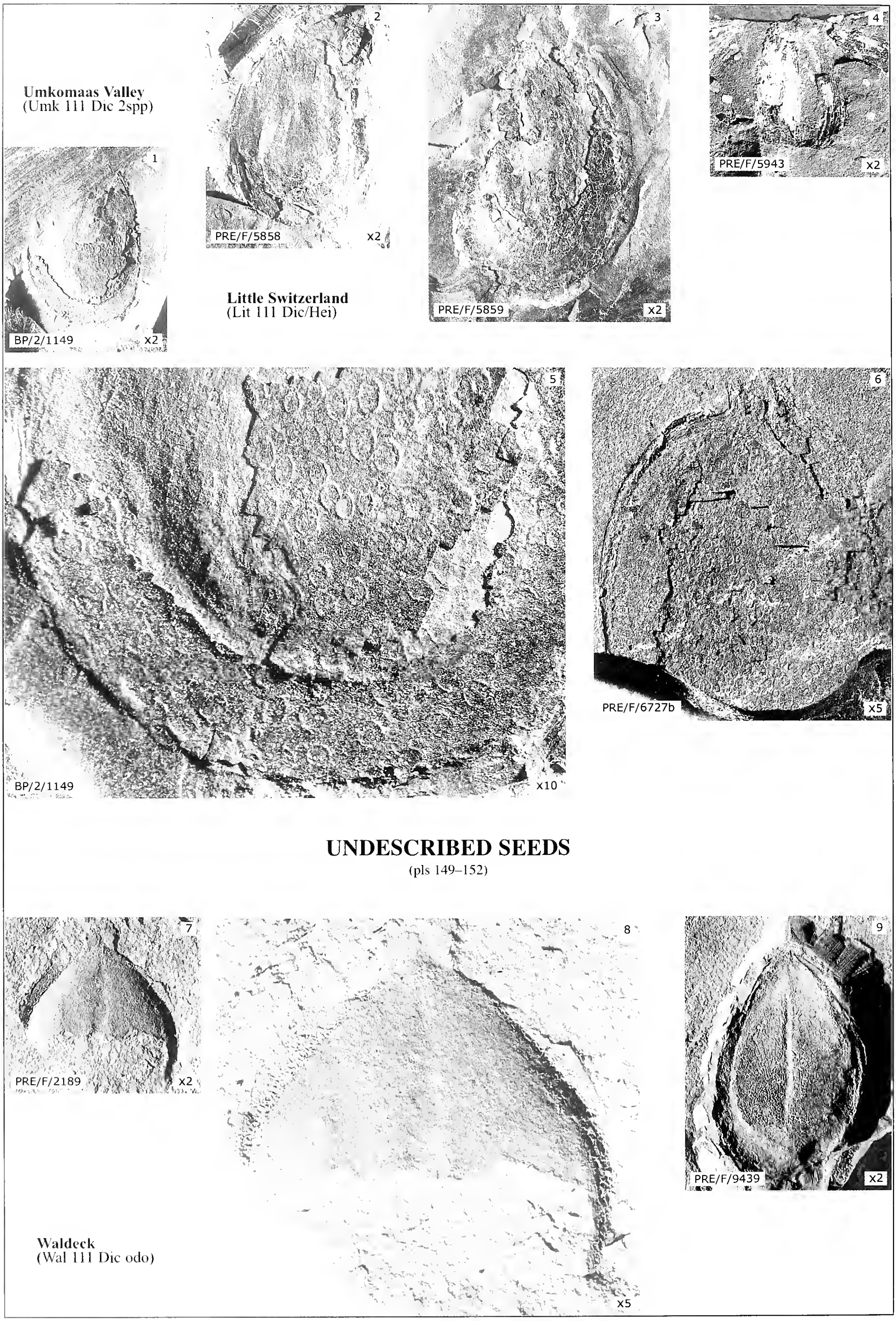






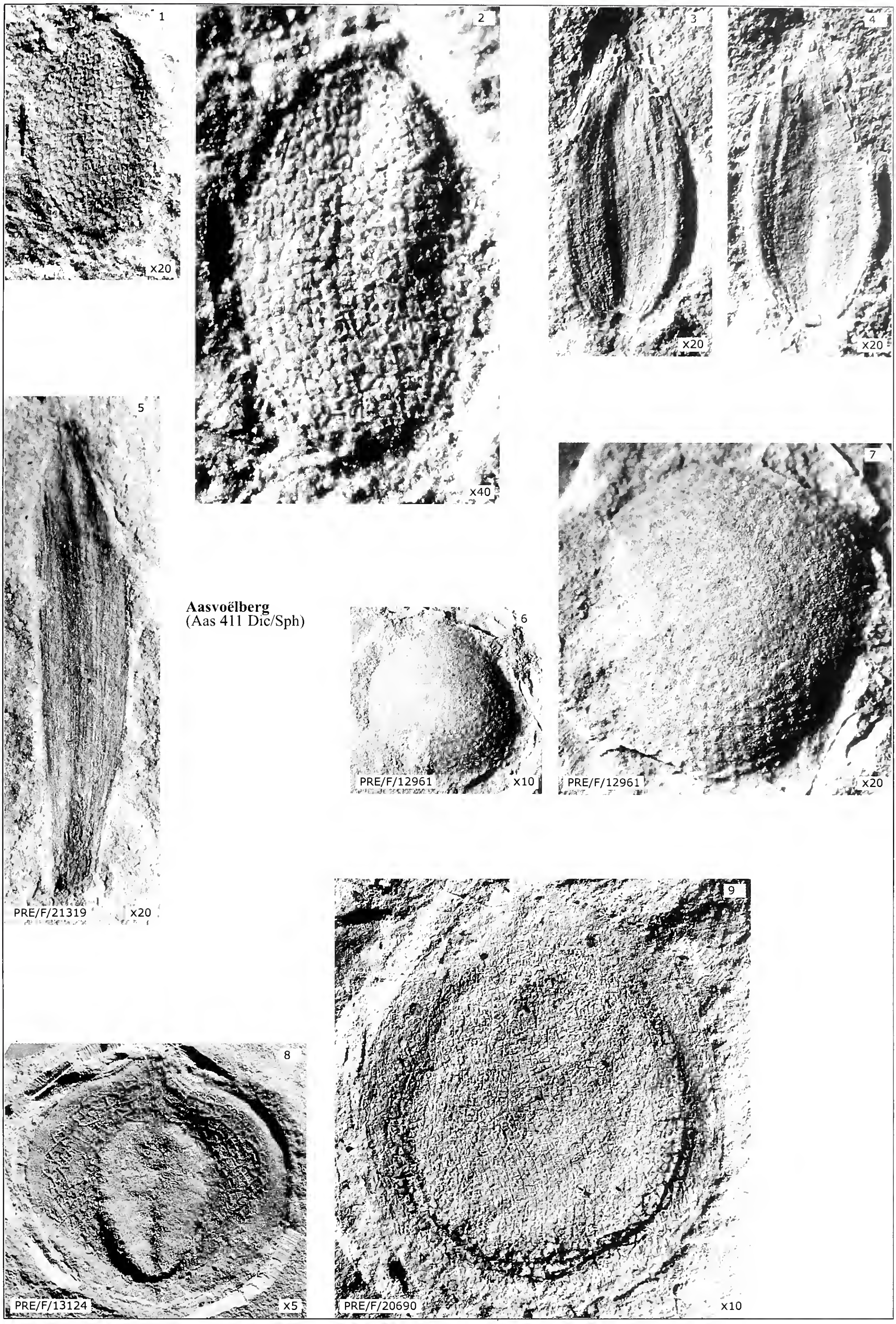


Jungites
showing the 2 species
from the Molteno
1
2
J. polymorpha
3
R3
x1
R3
x1
BP/2/1833
BP/2/1831
BP/2/1831
R3
x5
J. polymorpha
4
combination
of 2 photos
tfs 1–6 from
And. & And., 1989
BP/2/1842
?upper
x100
Lit 111
reference palaeodeme
Jungites spA
5
6
R2
x2
BP/2/1820
Lit 111
reference palaeodeme
BP/2/1820
?lower
x100



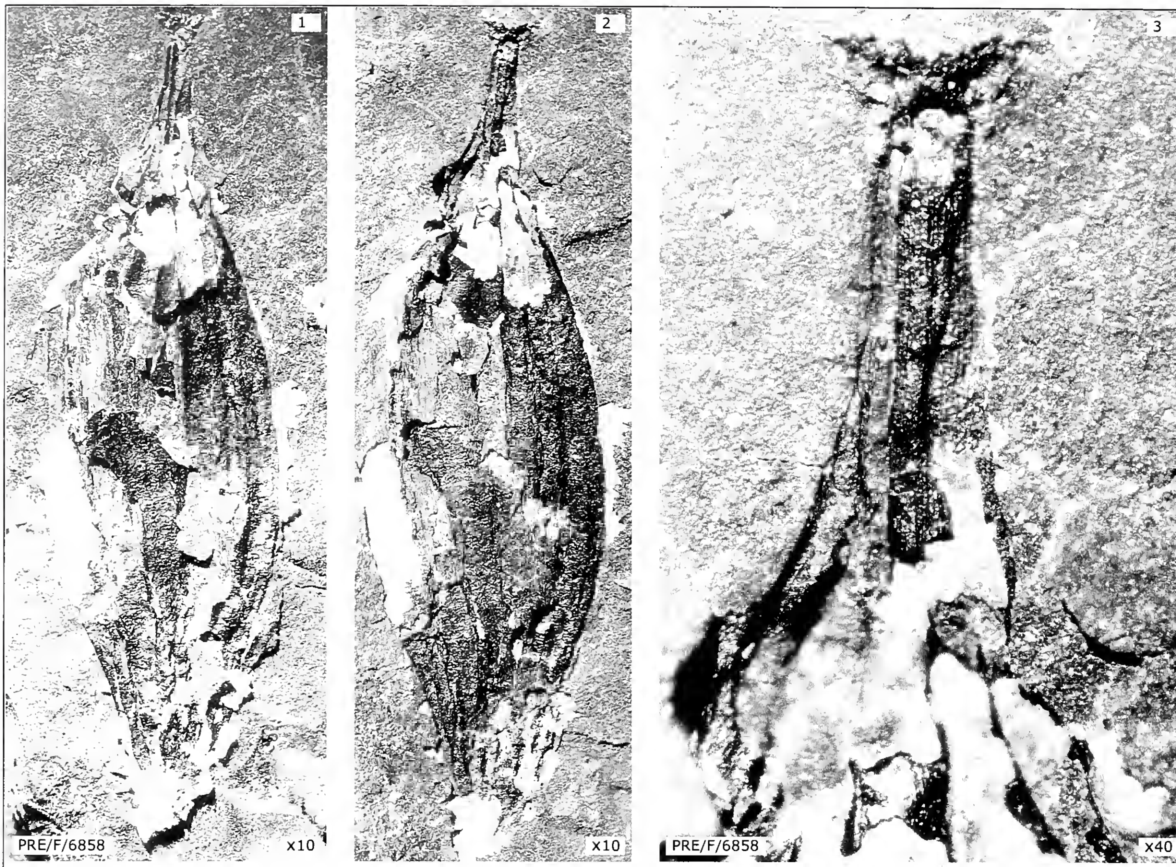
UNDESCRIBED SEEDS

(pls 149–152)

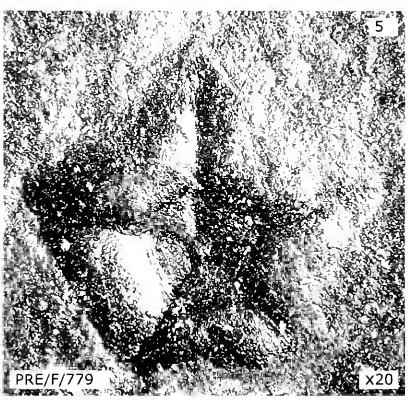


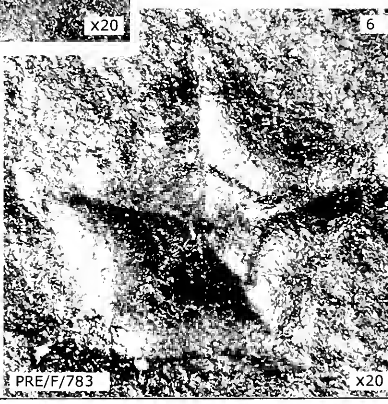
Aasvoélberg
(Aas 411 Dic/Sph)

INCERTAE/INCERTAE **pl. 150** **Undescribed seeds**

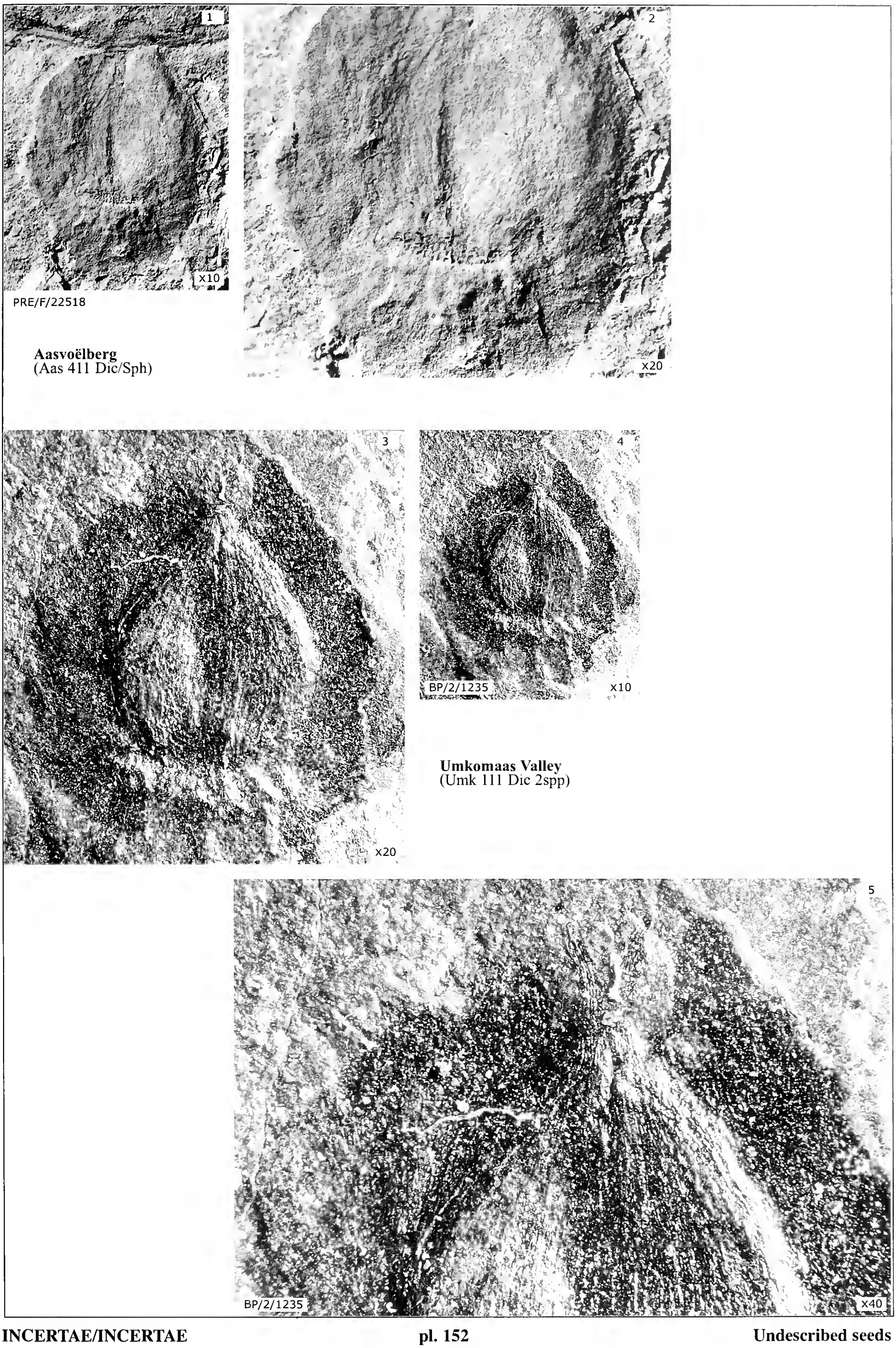


Little Switzerland
(Lit 111 Dic/Hei)





Umkomaas Valley
(Umk 111 Dic 2spp)


1
x10
PRE/F/22518
2
x20
Aasvoëlberg
(Aas 411 Dic/Sph)
3
x20
4
BP/2/1235
x10
Umkomaas Valley
(Umk 111 Dic 2spp)
5
BP/2/1235
x40

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GLOSSARY

The terms included here are those considered most relevant to our study of Molteno and Gondwana Triassic floristics and biodiversity. They are arranged to emphasise the significance of certain fields. A few terms are not applied in this book, but are retained for coherence of related topics. The glossaries appearing in the sequels to this work (Anderson *et al.*, in prep.; And. & And., in prep.) will be more comprehensive in certain fields such as 'Evolution and genetics'. Morphological terminology, covered in a pictorial key on pp. 50–53, is not repeated here.

**—terms introduced in our own works on the Molteno or other fossil floras of South Africa.

*—usage followed in our own works.

SAMPLING

Optimal sampling of fossiliferous strata—and there are many criteria that might be considered in defining optimal—is critical to reliable tracking of diversity patterns through time.

Frequency—The measure of frequency of a fossil taxon within a formation is the number of taphocoenoses (TCs) or assemblages, out of the total sampled, in which it has been found. Through the Gondwana Triassic, for instance, it might be the number of degree squares (out of the total sampled) in which it has been found. *

Abundance—The abundance of a fossil taxon is a measure of the absolute or relative number of individuals collected from or encountered in an assemblage, formation, region or continent. *

Assemblage—The full suite of fossil individuals or palaeodemes collected from a distinct lithological unit (lithosome) of limited geographic and stratigraphic extent. A megaplant assemblage will generally represent a localised mosaic of plant associations, less often a single association, through several generations. *

Locality—An area to about 1 km in diameter, which may include continuous fossiliferous exposure, but will generally include one or more productive exposures of lesser rank. *

Extensive sampling—Concerns the number and spread of localities sampled in a fossiliferous horizon. *

Intensive sampling—Concerns the comprehensiveness of collecting from a particular fossiliferous deposit. *

Singletons—Those species recorded from a particular geological horizon (member, formation or biozone) that are known from only a single locality. The number of singletons (and doubletons) is critical in projecting biodiversity from the observed record.

Doubletons—Those species recorded from a particular geological horizon that are known from only two localities.

TAPHONOMY

There is inevitably a reduction between the number of species making up the original flora and fauna of the region and that preserved in the fossil record. This filtering or winnowing of the original diversity occurs through the taphonomic process. Taphonomy is of vital concern in biodiversity projections. (Selected references: Ferguson 1992; Behrensmeyer *et al.*1992, Cuneo *et al.* 1993.)

Taphonomy—The conditions and processes intervening between a living species association and a fossil assemblage.

Taphonomic mode—Reflects the environmental context of the fossiliferous deposit. Examples include levee, lake, crevasse splay or abandoned channel of the floodplain (i.e. subenvironments of meandering and braided fluvial systems).

Isotaphonomic—Refers to fossiliferous assemblages of like taphonomic mode.

Biocoenosis—Living community. (p. 25)

Thanatocoenosis—Death assemblage; that fraction of the original community that is preserved in the fossil deposit. (p. 25)

Taphocoenosis (TC)—Taphonomic assemblage; fossil assemblage resulting from the taphonomic process; the aggregate of fossil remains contained in a deposit or bed.

Phytotaphocoenosis—A fossil plant assemblage or plant taphocoenosis.

Autochthonous—Describes TCs that have originated *in situ*. While such assemblages might be relatively common in the case of fossil tetrapods, they are a far more rare phenomenon in palaeobotany (e.g. horsetails entombed in growth position in a marsh).

Parautochthonous—Describes TCs deposited close to the original site of occurrence.

Allochthonous—Describes TCs deposited at some significant distance from the original site of occurrence.

PALAEODEMES

Terms either from And. & And. (1983) or our later works.

Palaeodeme (fossil population)—A collection of fossil specimens judged to represent a single potentially interbreeding population of plants or animals, showing a normal distribution of variation for selected diagnostic characters, and derived from a single taphocoenosis from a discrete small-scale lithological unit (lithosome) such as an abandoned channel infill or crevasse splay. **

Reference palaeodeme (RP)—The most comprehensive, representative, photographically documented palaeodeme in the literature proposed as reference for a particular infrageneric taxon. **

Reference assemblage (RA)—That assemblage from which the reference palaeodeme derives. **

Reference specimen (RS)—The most complete, average, mature specimen selected from the reference palaeodeme. **

Home palaeodeme—The palaeodeme from which a specimen derives. **

Sister palaeodeme—A palaeodeme belonging to the same species. **

FOSSIL TAXA

For form-genera and organ-genera, we follow standard usage. Further terms in this field are introduced, or used in a particular sense, to meet the specific needs of our Molteno research. The concepts can equally be applied to species.

Form-genus—'a genus of fossil plants based on a detached organ which, because of the limited characters shown, cannot be assigned to a family, although it may be possible to assign it to a higher taxonomic level. The "artificial" nature of such a genus is illustrated by the several instances where we have one form-genus in which different species may closely resemble members of two or more different families' (Jones & Rowe 1999).

Organ-genus—'a genus based on only part (an organ or organs) of a fossil plant, showing a sufficient range of distinctive characters that it may reasonably be assigned to a family. An organ-genus is regarded as "natural", in the sense that its constituent species are believed to have the same close relationship as those of a living genus. However, an organ-genus differs from a genus of living plants in that only fossils of the same organ, showing the same type of characters, can be assigned to it (e.g. fossil lauraceous leaves cannot be assigned to *Laurocarpum*, an organ-genus of fossil lauraceous fruit)' (Jones & Rowe 1999).

Whole-plant genus—A fossil-plant genus considered 'natural' that includes one or more organ-genera. The term is applied here only after comprehensive and systematic affiliation studies for the group (e.g. gymnosperms) and formation (e.g. Molteno) have been completed. In the Molteno (see Tab.15, p. 21), we recognise 38 gymnosperm whole-plant genera, i.e. 38 genera known from at least one of the three organs—ovulate, foliage or microsporangiate. (p. 43) *

Fossil-plant genus (or simply plant-genus)—A generalised term usually referring to a 'natural' whole-plant or multi-organ genus. *

Multi-organ genus—A fossil-plant genus considered 'natural' that includes more than one organ-genus. In the Molteno (see Tab.15, p. 21), we recognise 16 gymnosperm multi-organ genera, i.e. 16 genera known from at least two of the three organs—ovulate, foliage or microsporangiate. (p. 43) *

Mother-plant genus—The original living-plant genus occurring in the Molteno Biome. (The relationship between the living and fossil genus is akin to that between the phytocoenosis and taphocoenosis, i.e. between the living assemblage and the fossil assemblage.) *

Sister genera—Those organ-genera or whole-plant genera included in the same family or order (e.g. the three male-cone genera *Fredianthus*, *Lutanthus* and *Odyssianthus*, from the Molteno placed in the order Voltziales, pp. 70, 74). *

Sister specimen—A specimen of the same species from the same palaeodeme (e.g. as for *Lutanthus hemidiscus* and *L. ornatus*, p. 76). *

BIODIVERSITY

'The variety of organisms considered at all levels, from genetic variants belonging to the same species through arrays of species to arrays of genera, families, and still higher taxonomic levels; includes the variety of ecosystems, which comprise both the communities of organisms within particular habitats and the physical conditions under which they live' (Wilson 1992).

Observed diversity—The actual tally of taxa of a particular rank (e.g. species, families, orders) collected (curated and/or described) from a particular geological horizon (e.g. formation, assemblage zone). *

Preserved diversity—The projected tally of taxa of a particular rank representing the full potential sample (assuming comprehensive sampling of all preserved taphocoenoses) from a particular geological horizon. *

Existed diversity—The projected tally of taxa of a particular rank representing the full flora or fauna that actually inhabited the various habitats of the biome existing at the time of deposition of a particular geological horizon. *

Alpha diversity—The number of species occupying a particular habitat at a particular locality, e.g. the 73 foliage species recorded from the riparian forest at the Umkomaas locality, Molteno Formation.

Beta diversity—The rate at which the species number increases along a transect through adjacent ecozones (habitats).

Gamma diversity—The totality of species, considering all habitats over a broad area; e.g. the full extent of the Molteno Biome.

MNS (Minimum number of species)—The minimum tally of observed whole-plant species in a taphocoenosis, formation or other defined body of sediment. In the Molteno (Tab 15, p. 21), we recognise 143 gymnosperm whole-plant species: this is the sum of MNSs recognised for each whole-plant genus in the formation. *

ECOLOGY & PALEOECOLOGY

Biome—'A major category of habitat in a particular region of the world, such as the tundra of northern Canada or the rainforest of the Amazon basin' (Wilson 1992).

Ecosystem—'The organisms living in a particular environment, such as a lake or a forest (or, in increasing scale, an ocean or the whole planet), and the physical part of the environment that impinges on them. The organisms alone are called the community' (Wilson 1992).

Ecozone (habitat)—A physical or vegetational environment of a particular restricted kind, such as the riparian forests, braided-river sandbar meadows or floodplain woodlands of the Molteno Biome.

Guild—A set of species that live within a community in the same area and harvest the same food by similar means (Wilson 1992).

EVOLUTION & GENETICS

'Evolution proceeds mostly by the accidental substitution of one or more of the letters (of the genetic code), followed by the winnowing of these mutations and their combinations through natural selection' (Wilson 1992). The immense diversity of species derives from the astronomic number of rearrangements possible within the hugely lengthy sequence of nucleotide letters of the genetic code.

Evolutionary biology—Covers the broad array of disciplines—palaeontology, ecology, population biology, systematics, biogeography, ethology, cladistics, molecular evolution etc.—focused on the evolutionary process and consequently the building of biodiversity.

Hox genes—Those genes that control (encode) the body plans of embryos of all animals, apparently from the first multicellular animals some 700 Ma back to fruit flies, elephants and human beings today. All mammals, for instance, have 38 different Hox genes.

Genetic code—The code contains *ca* 1 million nucleotide pairs in bacteria and 1 to 10 billion pairs in higher plants and animals (Wilson 1992).

Macroevolution—'Evolution above the species level' (Stanley 1979).

Microevolution—Evolutionary change within the species (Stanley 1979).

Allopatric speciation (geographic speciation)—'The divergence to species level by populations that originally belonged to the same species but were isolated by a physical barrier such as a sea strait, river valley, or mountain range' (Wilson 1992).

Parapatric speciation—The divergence to species level by a local population while remaining in general contact with other populations of the original species (Stanley 1979).

Phyletic gradualism—Sympatric speciation. The evolution of one species into another through time. One species replaces another through a series of subspecies in an evolutionary lineage. Modification occurs through geological time in a single phyletic line (phylogenesis).

(This and the next two terms from And. & And. 1983, after Sylvester-Bradley 1977.)

Punctuated equilibria—Allopatric (geographic) speciation. A single species becomes ancestral to two or more descendant species through the splitting of the phyletic line (cladogenesis). Speciation occurs relatively rapidly such that transitional forms will rarely be preserved in the fossil record.

Reticulate speciation—Combines aspects of the previous two, involving both phylogenesis and cladogenesis. The central characteristic is the complex alternating isolation and hybridisation of races.

Extinction—The termination of any lineage of organisms, from subspecies and species to classes and phyla (Wilson 1992).

Renewal—Refers here to the re-establishment of diversity after a mass global extinction.

Adaptive radiation—'The rapid proliferation of new taxa from a single ancestral group' (Stanley 1979).

Evolutionary success (or prominence)—Can be measured in many ways, but is taken here as a combination of frequency, ubiquity, diversity, abundance and longevity—giving a **FUDAL** rating (And. & And. 1999).

Frequency—measure of repetitiveness of occurrence.
Ubiquity—measure of general range of occurrence.
Diversity—measure of speciation, radiation, variability.
Abundance—measure of quantity.
Longevity—measure of duration of the lineage.

In the Molteno Formation, for instance, *Dicroidium*, with a FUDAL rating of 188, was clearly the most successful plant genus, as it was throughout the Gondwana Triassic (pp. 26–29). *

CLADISTICS

Aside from its rigour in revealing phylogenetic relationships, cladistics has a major role to play in biodiversity studies. Consider current knowledge of mammalian and lepidopteran phylogeny: the cladogram, in each case, brings into focus a considerable hidden diversity during the earlier phases of adaptive radiation of the group (And. 1999).

Cladistics—Phylogenetic taxonomy; a rigorous attempt—with each step subject to Popperian falsification—to construct phylogenetic trees based on a selection of morphological and/or molecular characters with polarised (primitive or derived) states.

Phylogeny—The evolutionary history of a specified group of organisms of any rank, with particular focus on the genealogical tree of lineages comprising the group.

Cladogram—Figure or phylogenetic tree showing the branching pattern of the group under study.

Lineage—'A single line of descent' (Stanley 1979).

Clade—A cluster of lineages deriving from a common ancestor.

Monophyletic—Pertaining to a group of taxa sharing a common ancestor.

Polyphyletic—Pertaining to a group of diverse taxa not sharing a common ancestor.

Crown group—Includes the cluster of lineages expected to show all apomorphies (derived/advanced characters) of the extant taxa.

Stem group—Includes those forms (directly on the line to the extant group or on extinct side-branches) showing only some of the apomorphies of the extant taxa.

Sister group—That taxon or clade judged to share an immediate common ancestor with the group in question.

Plesiomorphic—Pertaining to the primitive state of a character.

Apomorphic—Pertaining to the derived state of a character.

INDEX TO CURRENT MOLTENO GENERA

The index includes only the generic names—ovulate, microsporangiate and foliage— retained in this volume for the gymnosperms of the Molteno Formation.

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"This remarkable book on the gymnosperms of the Late Triassic Molteno flora is a major contribution to understanding the diversity of seed plants that existed in the past. It joins the earlier works by the same authors in reflecting two lifetimes dedicated to exploring the biodiversity of the past so as to better illuminate the biodiversity of the present. . . . I am not aware of any other set of fossil assemblages that has been collected with such intensity, such uniformity of approach and such care. . . . By any measure, John and Heidi Anderson's dedication to unlocking the secrets of the Molteno Formation has been extraordinary and the result has been a landmark contribution to palaeontology." Peter R. Crane, FRS, Director, Royal Botanic Gardens, Kew, London, UK.

"The book is impressive in its scope and detail. It will represent an invaluable contribution to the palaeobotanical literature and will complete the description of the gymnospermous components of the Upper Triassic Molteno Formation—now the best studied Triassic flora on Earth. No previous palaeobotanical studies have provided such a comprehensive evaluation of the fossil-organ relationships between ovuliferous fruits, microsporangiate fruits and foliage from a formation covering such a large area and represented by around 100 fossil assemblages and around 300 000 specimens." Stephen McLoughlin, University of Melbourne, Australia.

"The prior volumes on fossil leaves have been invaluable, and set a new standard for thoroughness of documentation. . . . Few other publications can match their work as a scientific resource. . . . This next volume is arguably the most important of all as illustration of the reproductive organs will reveal the biological affinities of the plants. . . . It will form a fitting companion to the volumes already published and represents another monumental contribution." Gregory J. Retallack, University of Oregon, USA.

"It was 35 years ago, in March 1967, that I ventured for the first time into Molteno territory. From then till now the world has changed. It has shifted—dramatically—in virtually every respect: . . . Most importantly of all, from our perspective, the human population has doubled from 3 billion to 6 billion persons in this time . . . The Molteno became, increasingly, a lot more than merely an exercise in collecting and describing fossils. . . . It became part of a multifronted obsession to help swell our awareness of biodiversity trends through time, and to impact somehow on mankind's collision with that diversity as it exists today." John M. Anderson (from Preface).

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